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How Animals Find Their Way About

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How Animals Find Their Way About

A Study of Distant Orientation and Place-Recognition

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LONDON
KEGAN PAUL, TRENCH, TRUBNER & Co. Ltd.
NEW YORK HARCOURT, BRACE AND COMPANY
1928

MADE AND PRINTED IN GREAT BRITAIN BY
W. J. ROBINSON & CO., LTD., AT THE LIBRARY PRESS LOWESTOFT

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FOREWORD

ALTHOUGH, from the most remote times, the facts of distant orientation and the recognition of places have struck all observers, the solution of the problem set by these facts has occupied naturalists for scarcely half a century, and it is barely in the course of the last twenty-five years that systematic experimentation has arisen.

The investigations undertaken have had as their subject above all the Invertebrates, more especially the insects. On the Vertebrates we possess chance observations rather than rigorous and well-regulated experiments. It cannot then be said that the problem is completely solved. The data acquired nevertheless furnish important indications which permit the sketching of the outlines of the phenomenon, while bringing out also the gaps in our knowledge. Furthermore, the methods used to obtain positive data indicate the lines to follow in order to arrive at more numerous and more complete results.

HOW ANIMALS FIND THEIR WAY ABOUT

CHAPTER I

THE PROBLEM AND THE METHOD

LET us first of all state the problem

A bee comes out of the hive; it flies away, and then at some distance, often at a great distance, alights on a cluster of flowers and forages It goes from one flower to another, and works about in divers directions, describing many turns and meanderings, without any fixed order; at the end of a certain time, it flies off, and almost immediately takes the direction of the hive, which it regains by the shortest route.

An ant proceeds in an analogous way It leaves its nest, alone, as if it were walking at random; it follows a winding course until it encounters some booty or other. It then halts and returns, without marked hesitation, in the direction of the nest

The birds also do the same. They come and go away from the nest, fly about a little in all directions, but return constantly to their point of departure by the most direct way. Better still, the carrier pigeon, shut up in a cage, and transported to a point very far from the cote without perceiving anything of the route, is said to be capable of regaining the point of departure.

Numerous animals would appear to perform similar feats.

How do they discover or re-discover their way? What mechanisms enter into play?

Two hypotheses have been proposed.

The one resolves the problem in the simplest way. It supposes the animal endowed with an internal supra-sensory faculty which would render it capable of a veritable divination.

The other calls in the senses of the animal. Either the latter makes use of one or several of the organs of the common senses, its sensory memory—visual, olfactory, tactile, auditory or muscular—entering into play; or it utilizes a special sensibility permitting it to perceive elements of the environment imperceptible to man, such as electric or magnetic waves. The question is how to decide between these two hypotheses.

The hypothesis of an inner sense, as well as that of a special sensibility, escapes all direct research. On the other hand, the ordinary senses, well known to man, are immediately available. The most simple and sure procedure is, then, to organize our research on the assumption that these senses play a part. When the analysis is terminated with regard to them, we shall see whether they furnish the solution of the problem, or whether our investigations must be turned in another direction By elimination we shall perhaps arrive at a satisfactory conclusion.

Thus understood, the inquiry re-enters the domain of the biologist; it belongs appropriately and almost exclusively there. Indeed, this study should remain above all strictly *objective*, in the same way as the study of form or of function. If, in order to understand the facts observed, we fall back on our own experience, and compare the behaviour of the animal with that which we should have displayed in similar circumstances, we attribute implicitly to it our own sensations and perceptions Our analysis does not refer to its subject, and our conclusions therefore lose all value.

To avoid this danger, which renders all effort at solution ineffectual, it is important to maintain the research rigidly detached from ourselves We know the sensory end-organs of animals, as well as the various elements of the environment playing the *rôle* of stimuli. We are equally cognizant, thanks to its translation into motor terms, of the stimulation resulting from the interaction of these end-organs and the components of the environment.

Can we go further? Stimulation does not necessarily imply presentation; it has often for effect a pure reflex only. The movement of the iris under the action of light, for instance, is not vision. In addition, it is well known that in man every presentation corresponds to a sort of apprehension of the stimulus

—a sensation—and that the process is terminated by a co-ordination and elaboration of the sensations, which is perception. Does observation of the animal lead us to discover similarly in its case presentation, sensation, and perception?

The question merits our attention. On the answer we give to it will largely depend also the solution of the problem we have under examination.

Now, if we adopt for an instant the strictly psychological point of view, do we not, as soon as we go beyond stimulation, leave behind the realm of biology?

Is not presentation a fact of consciousness, and does not the inquiry then demand more than—or other than—strictly objective observation? Such a question has long since been raised. Piéron[1] attributes very rightly to Huxley[2] the merit of having been the first to explain clearly that the observation of the movements of animals in no way requires a knowledge of states of consciousness. Without denying them, we do not take them into account: we do not assume their existence. Whatever the appearances may be, they do not authorize us to formulate an hypothesis which would run the risk of modifying or of transforming the facts, and of falsifying the conclusions

When it is a question of orientation and of recognition of places, this biological attitude is imposed very specially. Often, indeed, and sometimes very markedly, the animals give the impression of effecting deliberate displacements, and of pursuing a well-defined aim. We have, nevertheless, no means of knowing whether this impression corresponds to any reality. And we shall avoid committing even a slight error by not assuming that there intervenes an intention, or a deliberation—a state of consciousness—of which we know nothing. In remaining objective, the experimental analysis will perhaps err on the side of deficiency, but it will always be easier to fill a gap than to rectify a fact distorted by the addition of imaginary data. In any case, the observed facts will suffice for the reconstruction of a mechanism.

In adhering to this rule, some difficulty will undoubtedly be experienced, and all the more because the language immediately suggesting itself to us supposes precisely states of consciousness. "willing", "seeking", "perceiving", "doing this *in order to arrive* at that", etc., are so many familiar locutions which we employ in describing our own behaviour, and which we do not hesitate to use when we describe the behaviour of animals. Doubtless the biologist employing them knows well enough what he means. But, whatever one might do, the words—the above especially—convey certain notions; and it is these that the reader or hearer will understand behind these words, in spite of all precautions. It is so simple to substitute the conjunction "and" for the prepositional phrase "in order to", and to describe the movements of an animal without saying that it is "seeking", "willing", or "perceiving". It is sufficient not to insert one's own experiences into the descriptions; not to add to the observed facts one's own sensations and perceptions. It remains true that he who wishes to do scientific work should avoid introducing into his research notions of which he cannot have direct experience, of which even the existence remains actually an unverifiable hypothesis.

To proceed thus is not, as some maintain, to diminish the value and significance of experimental analysis. It is, on the contrary, to give to it its whole power of penetration; it is to assure exact and complete results. It should be by elimination, and in so far as analysis fails, that we should have the provisional right to fill a gap in our knowledge by an hypothesis.

CHAPTER II

ORIENTATION AMONG FLYING INSECTS

HAVING thus established agreement as to the necessity for the objective method in the study of orientation, let us approach the study itself.

It is among the Invertebrates, notably among the insects, that the acquired facts are most numerous and significant. In many respects these organisms are more easily handled, and lend themselves with relative facility to varied experiments It is, however, necessary to distinguish among them those which move from place to place by means of flying, and those which do so by walking.

By very reason of the mode of progression, the problem presents itself differently. The animal which flies, naturally uses only some of its sense-organs; the animal which walks may, on the contrary, utilize them all, or even not use at all those which seem indispensable to flying animals

Let us examine the latter first.

With regard to them, a summary analysis is a necessary preliminary.

Current observation reveals that every bee that ceases foraging regains the hive at once by following a straight line, the "bee-line" This fact has been known for a very long time, and hunters of honeycomb make use of it to track down wild hives. They capture a first bee, give it a little honey, and then set it free. The direction taken by the insect being exactly noted, the hunters capture, a short distance away, a second bee, and proceed with it in the same manner. If the two bees belong to the same hive, they follow two paths which intersect at a certain point. This point corresponds to the site of the hive.

In the same way, bees captured in the vicinity of the hive, then transported and released at a point quite distant (2 kilometres, for example), set off immediately, taking the direction of the hive Gaston Bonnier [1] has established the fact beyond doubt.

These well-known facts furnish all the data of the problem. The return to the nest comprises three stages, which succeed one another without interruption. The departure in correct direction has in fact no useful result unless the insect recognizes the site of the nest, and then the nest itself. This constitutes three operations, which appear *a priori* distinct, and which must of strict necessity be examined separately: (*a*) departure in correct direction as far as the immediate vicinity of the nest; (*b*) recognition of the site, (*c*) recognition of the nest.

Do these three operations correspond or not every one to a special method of guidance? The affirmative seems very probable, at least as far as the bees are concerned. A summary examination permits us, indeed, to think that the first does not necessarily imply the two succeeding stages, and that the second does not any the more imply the third. The departure in correct direction is not to be confounded with the recognition of the site of the hive, for it most often happens that the bee, at the moment it ceases foraging, is unable to *see* the hive, it cannot even see the site. Sometimes the bee goes foraging several kilometres afield; in all cases, it goes far enough off to be separated from its hive by screens of trees, accidents of the land, or buildings.

In addition, proofs abound which oblige us to admit that the site of the hive is not for the bee confounded with that hive By displacing a hive to a distance of 1 or 2 metres, Turner[1] threw some bees off the track, and these flew about for a long time over the former site without re-finding the hive. Bethe[2] obtained the same results with even slighter displacement (50 cm). The insects came flying to the spot formerly occupied by the entrance, and the number of those finding the hive diminished with the extent of the displacement. As soon as the hive was brought nearer, they rushed on to it; they even entered any box put in place of the hive.

But they did not enter it at once; they manifested a certain hesitation. And this hesitation indicates clearly that, although the bees returned to the site, they did not accept forthwith the hive which happened to be there.

These facts are not confined to the bee. Many other nest-building Hymenoptera behave in an analogous way. To cite only the most recent instances, Deacy[1], in *Vespa vulgaris* and *Osmia rufa*, and Verlaine[2], in *V. vulgaris*, have observed similar manifestations for slight displacements of the nest (1 cm.). I for my part[3] have seen *Polistes gallicus* persist in remaining on the former site of a nest, newly placed at a distance of barely 25 centimetres. The attraction exercised by this former site was even such that the wasps sometimes passed right by the displaced nest without being arrested by it, at least at the outset.

It is, then, not the nest as such which serves as a landmark. The animal flies in the direction of a site which it does not normally perceive. In consequence, this movement in a general direction constitutes a first stage in the return to the nest; and this stage coincides with the actual problem of orientation.

A.—Movement in a general direction

Here the question arises—have we to do with sensory cues, or does the animal possess an inner sense of direction which guides it independently of all other means?

This latter hypothesis has been maintained by

Fabre[1], and by Bethe[1]; but their experiments carry no element of proof

Fabre used first of all some solitary bees of the genus *Chalicodoma*. Seven individuals were transported 4 kilometres away; four returned Fabre assumes that the three others were crippled specimens, damaged by the experimenter, or exhausted by the journey

In a fresh trial, forty individuals were transported 4 kilometres away, *about* twenty set out, two returned in forty-five minutes, having foraged, thirteen others returned after many hours

The lack of precision in these results surprises at once, so much does it contrast with the categorical tone of the conclusions Fabre knew nothing of the individuals which failed to return; he did not even know the exact number of those setting out; the length of time taken by the individuals which did return seems to him without importance

Two further series of trials failed to furnish more significant results Fabre transported to a distance a certain number of *Chalicodoma* enclosed in boxes; before releasing them, he subjected the boxes to rapid rotatory movements, with the object of confusing the insects The observations effected permit of drawing up the following table:

(a) Series in country of uniform aspect.

10	individuals	were transported	4 kilometres,	3	returned
10	,,	,,	,,	4	,,
50	,,	,,	,,	17	,,
20	,,	,,	,,	7	,,

(b) Series in broken country

40 individuals were transported 4 kilometres, 9 returned
15 " " 3 " by a complicated route; 7 returned
15 " " 3 " by a direct route, 6 returned

The disproportion between the individuals subjected to the experiments and the number of returns strikes one at once; it should inspire the greatest caution with regard to the conclusions. Furthermore, in no case did Fabre perform the necessary counter-experiment, which would consist in taking the insects, and leading them back to the same point of departure, in order to ascertain how many of them would return, and in what time they would do so. Satisfied with the results obtained, Fabre admits the existence of a "sense of direction".

Such mediocre experiments are not sufficient to sustain such an interpretation. In addition, analogous experiments made by the same author on *Cerceris* serve only to emphasize the extreme opposition which exists between the results obtained and the conclusions; establishing the return of four *Cerceris*, out of twelve transported to a distance of 4 kilometres, Fabre *assumes* that the others would return, and maintains a prudent reserve as to the reality of this return. Then he takes this experiment as a basis for rejecting afresh the hypothesis that the insect utilizes exterior cues, and insists on the existence of a "sense of direction".

Bethe, relying on experiments equally untrustworthy, though for other reasons, arrives at the same conclusion. He released in the town at Strasburg, in a street lined with high houses, and in the neighbourhood of his garden, two batches of bees, one of six individuals, the other of eight. Of the first batch:

Four bees set out in correct direction;
One bee set out in the wrong direction;
One bee set out in doubtful direction.

Of the second batch, all the bees started in correct direction, even before reaching the level of the housetops.

The fundamental fault in these experiments resides in the hypothesis, assumed as a fact, that the bees utilized did not know the town. Bethe assumes this without proof. Now, everything leads us to think the contrary. On one hand, the hive was quite adjacent to the place of release; on the other hand, Strasburg contains public and private gardens, and possesses shops selling sugar or similar substances, which cannot fail to attract bees. How could it be affirmed that the individuals used by Bethe had never traversed the streets and gardens, or visited the shops? The results obtained are not worthy to be taken into consideration.

An experiment of Sir John Lubbock[19] is the only one which could give any support to the idea of a "sense of direction". Lubbock placed a glassful of honey in a room lighted on two sides by windows; a nest of *Vespa sylvestris*[1] was situated outside in the direction of one of these windows, constantly closed. Through the other window, which remained open, a wasp entered the room, came to the honey, on which it remained for three minutes, and then flew off in the direction of its nest, towards the closed window. It circled round the room without succeeding in making an exit. Carried outside by Lubbock himself, it returned shortly afterwards, and departing again in the direction of its nest, knocked once more against the closed window. Five times in succession it behaved in the same manner. Lubbock would not seem far wrong in thinking that "the wasps have a sense of direction, and do not simply find their way by means of sight". This conclusion does not necessarily emerge from the facts. The author neglects to give us various important indications as to the arrangement of the experiment. Notably he neglects to say whether the closed window was not more lighted than the open one. The "persistence" of the insect in coming to knock against an insurmountable obstacle would seem due rather to some influence of this order than to a special inner impulsion. Moreover, the fact that the wasp finally learned the way back contradicts absolutely the conclusions of Lubbock. Does the "sense of direction" consist in taking a barred route, or in re-finding precisely the way which leads to the nest?

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[1] Lubbock gives the species as *V. germanica*.—Tr.

To sum up, the experiments from which the authors claim to draw the proof of the existence of a special sense, independent of cues furnished by the known senses, are hardly valid, and we are unable to retain them.

Quite on the contrary, rigorously conducted experiments point to a very different conclusion.

At the outset, a very general observation presents itself. Bees and wasps, at the moment of leaving their nests for the first time, rise into the air flying backwards, and move off slowly with their eyes turned towards the nest; they proceed in the same fashion when the nest has been moved Whatever may be the factor determining this behaviour, and whatever its true utility, it is quite evident that the insect has before it the image of the nest and its surroundings; the greatest probability is in favour of this image being registered We have here a preliminary assumption that the insect fixes sensory images

The insect next turns round and flies afield It comes and goes back and forth, hunting and foraging, and one is unable to put aside the further assumption that, all the time that it is on the wing, it is forming a visual acquaintance with the external world, that it is registering additional sensory images.

This registration, let us note well, does not in any way imply the intervention of states of consciousness. We have proof of this from our own experience; and this is exactly one of the rare circumstances in which our introspection can aid in the analysis of the process. We are constrained to recognize, in effect, that we often see without looking, that we register images of objects to which we give no conscious attention. To suppose the animal endowed with a capacity which is exercised with precision independently of conscious states is not, then, to formulate a gratuitous hypothesis, nor to attribute to it specifically human qualities.

The facts, moreover, agree in showing the reality of the visual cues which the initial observations enable us to predicate.

The experiments of von Buttel-Reepen furnish a first indication He transported a hive 7 kilometres from its original site, and then captured several bees before they had been able to emerge and circulate in the new region He liberated these bees in groups at distances from the hive varying between 40 and 80 metres Whenever an obstacle—tree, house, or thicket—was found to be interposed between the point of liberation and the hive, the bees were incapable of finding the way On the other hand, all the bees which had been able to emerge from the hive regained it when released under similar conditions. The latter, it must necessarily be admitted, had acquired knowledge of places of which the former remained in ignorance.

It is, moreover, unnecessary to move the hive in order to perform similar experiments; it is sufficient to utilize, as von Buttel-Reepen also did, young bees which have never been outside the hive Released even a short distance from the latter, not one returns. The experiment can be varied by releasing bees not far from the hive at twilight; they describe several circles in the air, and soon drop, definitely lost.

Several years before, Romanes[11] had made an analogous experiment Placing a hive about 300 metres from the coast, in a building situated in the midst of very large gardens, he allowed the bees time (one day) to explore the immediate vicinity He then shut the hive, and captured a certain number of individuals, which he divided into two lots He released one of these 250 metres away, on the seashore outside the gardens, and the other at the actual extremity of the gardens Of the first lot, no individual returned; of the second, all returned rapidly.

In the same way, Yung[12] transported to a distance of 3 kilometres on the Lake of Geneva, a batch of bees taken from a hive situated on the shore of the lake. These bees did not return. On the other hand, a second batch, belonging to the same hive, was transported 6 kilometres inland, all the bees returned.

These facts seem highly significant Not only does none of them suggest the idea of a special sense, but all lead to the conception of visual cues The bees wander as soon as they are released in an unknown region.

Experiments with wasps give concordant results. Gathering the entire population (25 individuals) of a nest of *Vespa sylvestris*[11] suspended in a bell-jar having a tubulure (fig 1), I released them 50 metres from the nest, in a locality where they were apparently in the habit of circulating (fig 2, *A*) The first had returned at the end of two minutes, 19 had returned in succession at the end of an hour and forty-five minutes, two only were definitely lost Three hours afterwards, the 23 wasps were transported 200 metres from the nest into a totally different locality, a house interposing itself between the nest and the place of release (fig 2, *B*) The first return did not occur until eleven minutes and forty seconds had elapsed, the fifth after sixteen minutes; the thirteenth after two hours forty-five minutes; 11 individuals were definitely lost.

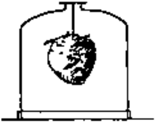

FIG 1.—Nest of *Vespa sylvestris* suspended under a bell-jar with a tubulure

The thirteen wasps which returned were carried back the next morning to the same spot. All returned, the first in seven minutes, carrying booty; the fifth in twelve minutes; the sixth in thirteen minutes with booty; the thirteenth in one hour forty-five minutes.

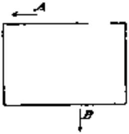

FIG 2.—Directions of liberation of *V. sylvestris* A, at a distance of 50 metres from the window before which the nest is placed. B, at a distance of 100 metres from the other side of the house

These three series of tests are conclusive. They show clearly that the return to the nest coincides for the wasps with the knowledge of places, and this implies an apprenticeship. In a known locality, the return is immediate and the number failing extremely low, in an unknown locality the return is lengthy, and the failures considerable. The individuals which have finally found their way make the journey more quickly a second time, and there are no failures.

This knowledge of places is, and in the case of the departure of flying insects in the right direction, can be due only to the registration of visual cues. What are these cues and what is their nature?

Other experiments furnish on this point definite data for a satisfactory approximate explanation.

Ferton[16] observed a solitary bee, *Osmia rufohirta*, which nests in the shells of a snail (*Helix pisana*).

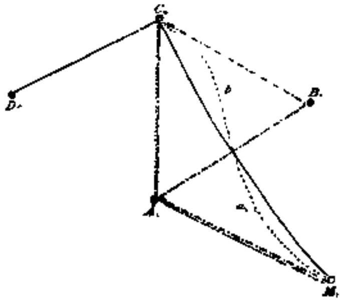

FIG 3.—Successive paths of *Osmia rufohirta*.—*A*, *B*, *C*, *D*, successive positions of the nest. *M*, plant on which the *Osmia* forages (after Ferton)

The nest was at *A* (fig. 3), while the bee, foraging at *M* on a plant tuft, travelled constantly over the path *MA*. At a given moment the *Osmia* transported the shell to *B*, 12 centimetres from the original situation. Continuing to forage at *M*, it did not return directly from *M* towards *B*, but made an angle in the direction of *A*. The observer then carried the shell to *C*, 12 centimetres from *B*. The *Osmia*, returning from *M*, beat round for a certain time and at length found the shell. It returned to forage at *M*, and on its way back took without alighting, but in marking a pause at the level of *A* and *B*, the course *MABC*. Next, of its own accord, the *Osmia* replaced its nest at *A*; then from the tuft *M* it set out in the direction of *A*; without having reached this, it made, at the point *a*, a curve towards *B*; arrived at the point *b*, it described a new curve and arrived at *C*, whence it set off towards *A*. The bee thus traversed, without alighting, the traject *MabCA*. At last Ferton carried the shell to *D*; the *Osmia* then followed the line *MACD*, but soon rectified the route and took the line *MCD*.

The same worker performed an entirely interchangeable experiment with another *Osmia*, *O ferruginea* The results obtained led him to conclude that the insect registers certain visual *images*—the local topography of the points *A*, *B*, *C*, *D*

These facts, nevertheless, might authorise equally well another conclusion. Taking into account the fact that the *Osmia* passes each time by the points where the nest originally was, Piéron [11] enunciates the hypothesis of a *muscular memory* (kinæsthesis). He considers that the insect would register, not visual images, but a certain effort brought about in a certain way. To this interpretation Ferton[14] firstly opposes the argument that the bee does not always follow exactly the same path, but *loosens* its curve more or less, a fact which exacts a different effort at every journey; and secondly, he supports this argument by a fresh experiment. A nest (shell of *Helix vermiculata*) of *Osmia rufohirta* was situated (fig. 4) in a small bare space, a little in front of some tufts of grass *MN*; the bee was foraging at *D*, 3 metres away; some plants of *Cistus*, *U*, *V*, *X*, *Y*, *Z*, lined the way between *D* and *MN*. Ferton moved the shell to *B*, 30 centimetres away; after some turns and wanderings the bee re-discovered it, and from this moment traversed the course *DM-NB*. It thus behaved as did the preceding insect. The question is, precisely, to know whether the form of the course pursued depends on muscular memory or on visual cues. If these latter exist, they were perhaps taken from the tufts of grass *M* and *N*; Ferton cut them off and pulled up also the neighbouring grass. From this time, the *Osmia* flew towards the site *MN* as long as it found itself between the tufts of *Cistus*; immediately afterwards, it turned straight towards *B*. It was then, in the absence of *M* and *N*, at once attracted by *B*. It is indeed a question of visual cues, consisting of various features of the landscape in the midst of which the bee is flying. The conclusion is important, but it only touches part of the question.

These same experiments permit us to estimate the way in which the flying Hymenoptera make use of visual cues. In sum, these cues are linked together on the return in the inverse order from that in which they were connected on the outward journey. Every one suggests the next following. Repetitions of the same journey always result in simplification; certain cues are neglected, then omitted, and a new order is established. This emerges clearly from Ferton's first experiment. It follows

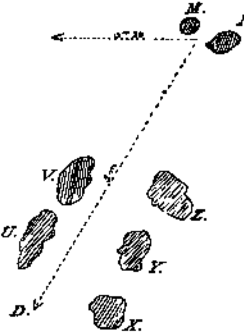

FIG 4.—Course of *Osmia rufohirta* between some *Cistus* (after Ferton)

also from the second, since this shows that the suppression of an intermediate cue, far from putting the insect off the track, leads it simply to associate two images not originally consecutive—it "tautens" and straightens its course.

An observation by Descy[4] permits us to isolate the process. An *Osmia* (*O. rufa*) has just finished a nest (*A*), and commences another (*B*) a metre away. It forages on a neighbouring tuft. Going from the tuft to *B*, it passes by *A*. At the beginning it rests on the finished nest; but, in the course of successive journeys, the halt becomes more and more brief, until finally the *Osmia* no longer stops.

Thus is constructed the "bee line"—the course of return in a straight line. This is not all; one can well conceive that starting from a certain cue situated quite far from the nest, in the zone where the insect is foraging, the greater part of the cues become finally neglected, and there are substituted little by little for the visual images previously registered, other images, this time of a muscular order. All takes place then as if, a point of departure being given, the bee or wasp registered a certain effort, and set off without using a whole series of visual cues; the route for them is no longer marked out except at long intervals.

In certain circumstances, however, and for short journeys, muscular memory seems to be installed almost at the outset, and to play an exclusive *rôle* as the means of return. When various *Ammophila* dig their burrow, they remove the débris with their mandibles and carry it by flying to a distance of 50 or 60 centimetres, coming and going a great number of times The observations I have made on *Ammophila heydeni* [11] have immediately suggested to me this interpretation. The wasp moves off in a straight line, deposits its burden, turns round and returns in a straight line Every time it goes from the burrow an approximately equal distance There exists nothing, to left or to right, which could serve as a cue, and other circumstances, to which we shall have to return, allow us to affirm that neither does the sight of the nest act at all in this way Descy [14] and Verlaine [1] have made analogous observations, and arrive at similar conclusions For his part, Ferton [11] finds that, at the beginning, the *Ammophila* does not alight exactly on the burrow; precision is established in the course of the successive returns, and is lessened by a contrary wind This last indication supports clearly the idea of a kinæsthetic memory substituting itself for visual cues, in increasing the effort to accomplish the distance, the resistance of the wind shortens the journey effected by the *Ammophila*

B.—Recognition of the nest site

Thus guided by the kinæsthetic cues which are substituted, in part at least, for the visual ones, the flying Hymenopteron arrives at the site of the nest.

Does the recognition of this site coincide with the finishing of the journey? Is muscular memory sufficient; or does this recognition demand the constant use of visual cues?

We have already indicated in a general way that the insect finds the site in the absence of the nest itself. Thus stated this fact would lead us to think that the Hymenopteron associates the topographic position of the nest with the end of a muscular effort. Certain more precise observations therefore become indispensable, in order to show that the site of the nest is in reality associated with sensory cues, and that it is perhaps not itself one of these cues. As a matter of fact, the cue which guides the insect is not always the one which most attracts the observer's attention. When the latter perceives an object near the nest, or is struck by a certain disposition of the surroundings, he is tempted to attribute to that object or that disposition a great importance, whilst the insect may appear hardly affected by the one or the other. Such is the case of the *Bembex rostrata* observed by Bouvier[illegible]. Ten centimetres away from the orifice (*A*) of the nest of this *Bembex* was a stone (*P*), which seemed a characteristic feature of the surroundings (fig. 5). Nevertheless, the transport of this stone, either to *A* or to a position in symmetrical relation to *A*, did not occasion any perturbation on the part of the insect. On the contrary, *when the stone was replaced in its original position*, and all the space around the nest sanded, the *Bembex* wandered for forty-five minutes or more without discovering the entrance. The stone therefore did not act as a cue; this resided doubtless in some local disposition not recognized by the observer, but which the insect registered exactly.

In the same way, another observer demonstrates that it suffices to mow down the grass around the openings of nests of *Bombus* in order to disorient the insects. In proceeding thus, however, one does not know exactly what one is doing; for as Verlaine[1] remarks, modification of the site of the nest produces no clearly appreciable effect on *Bombus lapidarius* and *B. hortorum*.

In many cases, however, the experimenter discerns these cues, and can assure himself that they are undeniably of a visual order. Marchand[11], for example, observed the opening of a nest of *Bembex* situated 50 centimetres in front of a tuft of *Vincetoxicum officinale*; he cut off the tuft and placed it 60 centimetres to the rear. The *Bembex* returning to the nest was disoriented; on the other hand, it went straight to the nest when the tuft was replaced at its habitual distance. Everything took place as if the tuft of *Vincetoxicum* were the exterior sign of the nest.

Ferton[21] similarly observed a *Eumenes pomiformis* provisioning its nest, which was constructed on the branch of a broom plant He cut off one branch to the right of the nest and another to the left. This modification had the immediate effect of completely disorienting the Hymenopteron.

In certain circumstances, the modification effected seems at once more insignificant and more precise in its effect. Thus, an *Osmia rufa*, studied by Descy[*], had built its nest in the angle of a wall one centimetre away from an iron spike, fixed in the wall, and projecting from it about ten centimetres. As long as things remained undisturbed, the *Osmia* came and went regularly. In the absence of the *Osmia* the iron spike was taken away; when the bee returned it wandered about, flew past the entrance of the nest, and disappeared. Then the spike was replaced; the *Osmia*, which had not ceased wandering round, returned at once. During a fresh absence, the spike was taken out and fixed a little lower; this simple displacement equally confused the insect.

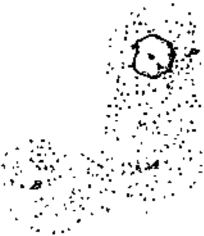

FIG. 5.—Observations on *Bembex rostrata* (after Bouvier)

I had previously made an analogous experiment[11]. An *Ammophila heydeni* was digging its burrow on the floor of a fairly deep excavation, made in a sustaining wall to allow the draining off of water (fig 6) At intervals the insect ceased excavating and flew off, receding from the wall, following a line at right angles, and carrying in its mandibles some particles of earth It deposited its load 50 or 60 centimetres from the wall, and then returned in a straight line towards its burrow. Always similar, this movement seemed stereotyped, and I have indicated above that the insect was obeying in all

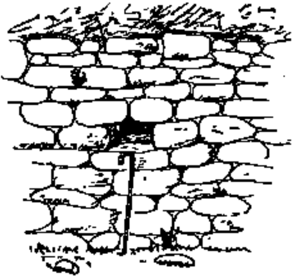

FIG 6 —Experiment with *Ammophila heydeni*.

probability its muscular memory. But this is valid only for the journey leading straight towards the wall. Here is the proof. During one of these short absences I tore up some tufts of *Sedum* which were growing near by, and placed them within the border of the hole, on the edge, but not projecting beyond the surface of the wall. On returning, the *Ammophila* hesitated very slightly, but nevertheless went straight to the burrow, emerging again shortly afterwards. I profited by this to add in the same conditions some supplementary stalks of *Sedum* and some dry leaves. The behaviour of the *Ammophila* was in no way changed. Then, taking away stalks and leaves in the absence of the insect, I propped against the wall, at the level of the lower edge of the hole, a walking-stick with a crook, in such a way that the crook projected directly forwards. The insect, which had just deposited its load of earth, returned directly towards the wall, but arriving near the crook it stopped, turned briskly to the right, proceeded to alight on the wall one metre fifty centimetres from the hole, and then set out again and disappeared. It returned at the end of half an hour; the stick having been taken away, it entered the hole directly and began to dig. During this time I replaced the stick, and when the *Ammophila* emerged it walked *along* the crook; on its return it halted again, flew to the fixed point *in front of* the margin of the opening, then turned to the right and disappeared. An hour afterwards it had not yet returned.

According to the evidence, the cue is not here the actual opening of the hole; its form and its interior arrangement do not appear to be connected with the burrow in course of digging, since modification of the aspect of the opening produces no serious effect. It is much more probably the whole of the surface of the wall which constitutes the cue leading immediately to the burrow or nest, and which guides the *Ammophila* in the same way as the iron spike marked the last plane encountered by the *Osmia*.

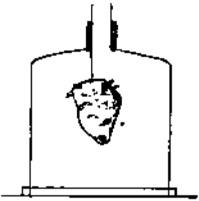

FIG. 7.—Experiments with *Vespa sylvestris*. The tubulure of the bell-jar containing the nest is lengthened 5 centimetres.

To sum up, the cue appears to be less an object taken by itself, than a topographical relation between various objects and the nest.

This interpretation seems especially imposed in the presence of the following facts relative to *Vespa sylvestris*. I had installed a nest of this species (fig. 7) under a bell-jar having a tubulure at the top; the bell-jar was placed before an open window; the wasps entered and emerged freely, foraging and hunting in the surrounding countryside. This arrangement permitted me to proceed with various experiments”. Ordinarily, on returning from without, the wasps landed directly on the upper orifice of the tubulure, alighting without hesitation on the rim of this opening and going within immediately.

Where is the cue in this case? Is it the relatively voluminous bell-jar? What would happen if the tubulure were displaced? First of all I moved the bell-jar twenty-five centimetres nearer the window, while a certain number of wasps were absent. On their return, instead of going straight on to the mouth of the tubulure, they passed beyond it without stopping, and circled round for several moments before finding the bell-jar and its opening. Then the bell-jar being in its usual place, I fixed in the tubulure, by means of a cork, a glass tube which had the effect of raising the neck five centimetres (fig. 7). The operation was effected, like the preceding one, whilst a certain number of the wasps were absent. When they returned, all except one alighted directly *at the level* of the normal opening of the tubulure, which was closed by the added tube. Confused, the wasps crawled round for a variable time, and finally went up to the level of the new opening. I varied the experiment by raising the bell-jar a distance equal to its own height (20 centimetres), without introducing any other modification; this time the wasps alighted directly on the edge of the platform, which occupied the former level of the opening.

Must kinæsthesis be advanced as the cause? If one considered only the first experiment, where the wasps flew beyond the bell-jar which had been brought nearer, one could suppose such to be the case. But the inverse experiment, consisting in moving the bell-jar further off, does not agree with this interpretation If, in short, the wasps, guided by muscular memory, go beyond the bell-jar when it has been brought nearer, they ought to circle on the previous site of the bell-jar when it has been moved backwards. This is not what happens; the wasps arrive at the tubulure without perceptible hesitation. Moreover, how can kinæsthesis be said to intervene when it is above all a question of level? One can hardly suppose that the wasp returning from the fields flies always at the same height, and in such a way that a certain effort corresponds with the arrival on the bell-jar.

In reality, everything takes place as though the wasps measured, on the one hand, an angular distance between the two planes—the plane of the table and that of the opening—and on the other hand, a relation of distance between the successive vertical planes It is not the nest which is seen, which is separately localized, its position is established, for the wasp, in relation to the objects determining planes superposed in the horizontal sense, or successive in the vertical one.

Therefore, every displacement of the nest, or every modification in the plane levels, should cause confusion, and if the experiment of removing backwards produces no perceptible effect, this is due doubtless to the fact that the wasps, carried on by the impetus of their acquired speed, arrive straight on the bell-jar. But a lateral displacement would have sufficed to confuse the insects. This is what Verlaine[1] observed when he effected such a displacement of a nest of *Vespa sylvestris* in relation to a tree.

In addition, one last experiment shows the reality of this localization by successive planes. The shutters of the window in front of which the nest was situated were generally wide open, and swung back against the outer wall during the day; if they were completely shut, the wasps entered by the space existing between their lower margin and the window ledge without manifesting any confusion. But it sufficed to leave the shutters half closed, making with the wall an angle of 100° to 110° to confuse the wasps greatly. The position of the shutters forms, then, a supplementary plane before the wall. It is the same *rôle* as was played by the walking-stick in front of the hole of the *Ammophila*, or by the iron spike beside the nest of the *Osmia*.

The recognition of the nest site thus depends incontestably on visual cues, which cease at no time to direct the insect. In the course of journeying in the direction of the nest, the various visual memories have been able to become effaced, and to give place to muscular memory; in the vicinity of the nest, kinæsthesis no longer plays a part, visual cues again intervene, and everything seems to indicate that the site itself is recognized only in close connection with these cues.

It is, moreover, a question of a complex chain of events such that the cue is no longer the nest as an object taken by itself, but a relation of distance between various planes marked by the object or by the nest. Furthermore, the Hymenopterous eye perhaps does not give a clear-cut, nor above all a detailed vision of objects. The *Ammophila* seems scarcely able to distinguish the change caused in the general picture of the opening at the bottom of which it is excavating its burrow, but it distinguishes at once the presence of the object which, placed in front, modifies the registered distance. It is thus also in all the other cases. The insect appreciates superposed or successive groups of objects and their relations of distance; the isolated modifications of a part of any one of these groups passes as it were unperceived, whilst the interposition or suppression of a new group occasions a lengthy confusion.

C.—*Recognition of the nest*

Does the arrival at and recognition of the nest site lead to the recognition of the nest itself? If the nest which happens to be on the site is not the real one, will the insect adopt it without difficulty?

When apiarists wish to reinforce a swarm or to change a hive they substitute one hive for another, and the bees generally accept the substitution. Does it follow that for the bees the nest is identified with the site? A categorical affirmation would perhaps not correspond with the truth. Even when it is successful, the substitution effected by the apiarist induces a certain disturbance among the bees, which do not at once adopt the new hive. I have been able to assure myself with other Hymenoptera, that if the insect finds another nest in the place of its own, the change does not leave it entirely indifferent.

It was with this aim that I substituted for the bell-jar covering the nest of *Vespa sylvestris* another, similar in every particular, covering a nest of *Vespa crabro*. At the moment of substitution, several *Vespa sylvestris* were foraging in the fields. Two of them soon arrived, they went indeed into the new bell-jar; I remarked, however, a slight backward movement before entering. Once in the bell-jar they went on to the nest, but stayed hardly a moment, and then departed. Evidently the extreme similarity of the two bell-jars led to confusion, which was produced without being exactly immediate, but which stopped at this point and did not extend to the nest.

In the same way, I substituted for a nest of *Polistes gallicus*[*] a nest of the same species, empty and dating from the previous year. The *Polistes* returning to the site alighted on this nest, "explored" it, and finally abandoned it. Certainly, this nest no longer contained any larvæ, and so differed essentially from the actual nest. Perhaps this circumstance determined the abandonment, as Descy has suggested[28].

The experiment, when made under improved conditions, gave results very little different. In the course of the summer of 1925, I placed side by side the nest from which a *Polistes* had just emerged, and another which was still in use. Set down an equal distance from the two nests, the insect "explored" them one after the other, and finally abandoned the strange nest.

Another equally positive observation shows that changes very slight in appearance occasion an "uneasiness" on the part of the insects. When I added a tube to the neck of the bell-jar enclosing the nest of *Vespa sylvestris* (v. p. 32), this addition had not simply the effect of raising the opening and confusing the wasps; it provoked also a marked hesitation once the new opening was discovered. Not all entered directly—at least they became involved in the added tube and came out again. Conditions were evidently not as usual. Several wasps, nevertheless, entered without perceptible hesitation.

On the other hand, the wasps which were in the bell-jar when I inserted the tube manifested a great uneasiness. Though the added tube simply reduced the calibre of the opening without obstructing it, all the wasps massed themselves finally at the level at which the tube entered the bell-jar. Some went into the tube but immediately came out again, as if they found an insurmountable obstacle before them. It was only at the end of half an hour that the insects overcame this difficulty It cannot be doubted that the new arrangement, whether because of the slight ledge caused by the tube, or the calibre of this tube, or some odour—or any other analogous cause—prevented the wasps from "recognizing" the orifice by which they had for several days been leaving the nest.

It is true that the substitution or modification effected does not always provoke a marked uneasiness. I refer to the fact that Descy was able to replace a nest of *Vespa germanica* by another without causing any confusion Substitution is always possible, since apiarists are constantly making use of it, but this does not mean that it occasions no reaction, or that the new nest is adopted at once From the assemblage of facts, the likelihood emerges that the insect does not confuse nest with site, but recognizes the nest.

What then is the cue to the nest? We have hardly the means of choosing among all the various possible hypotheses. The experimental data solely enable us to say that sight does not undeniably play the preponderant *rôle*, and that olfaction intervenes perhaps in a more active way. It seems difficult, in fact, to admit that the Hymenopterous eye discerns such a minute detail as the modification in thickness of glass, or the very slight difference in contour between two nests of the same species. Moreover, the facts observed by Ferton in the *Osmia*[14] indicate clearly that only the colour and shape of the *ensemble* affect these insects. When one moves the shell in which an *Osmia* (*O. rufohirta*) has made its nest, the insect comes and goes, turning in all directions; at intervals, it alights on shells, or even on stones of similar colour. Giard[15] has also made similar observations on *Osmia aurulenta* nesting in the *Helix* of the dunes of Wimereux.

In all probability, the visual images registered by the *Osmia* are images of an *ensemble* corresponding to a contour of vague shape, or to a not very clearly defined system of coloration. The cues permitting effective recognition are furnished by other senses than sight. In the case of the wasps frustrated by the addition of a simple tube, these cues are perhaps of a tactile order. In the case of the *Osmia* of Ferton, they are, in part at least, of an olfactory order. Scarcely has the *Osmia*, in fact, alighted on a stone, or a strange shell, than it departs at once and recommences its wandering; when it alights on its own shell, it recognizes this immediately. It recognizes its shell, even if the shape has been changed, either by damaging the peristoma or by partial burying in the ground; it recognizes its own in the midst of many others, even if it is crushed. A distinction, however, is necessary, which clearly defines the process. Recognition takes place when the peristoma is above, but not, according to Ferton, when it is below, and when the emanations from the bee-bread are thus either stopped or at least strongly diminished.

The recent experiments of Verlaine[44] reveal equally the part played by olfaction in this "recognition" of the nest The experimenter concealed a nest of *Vespa germanica* under a cardboard shade, and disposed all around ten similar shades. The relative position of the nest was constantly modified in such a way as to avoid topographical localization on the part of the wasps The cover of the nest was, however, perfumed with mint or eau-de-cologne. The results were very significant; although availing themselves of no other cues than the odour exhaled by the cardboard shade, the wasps returned straight to their nest Verlaine[7] had previously established the fact that if their nest is suspended from a branch of a tree, wasps are attracted by it when they find themselves beneath it, at a short distance, in a head wind.

Observations and experiments thus agree Positive for both *Osmia* and wasps, they carry some degree of generality. It is true that not all flying insects have an equally developed sense of smell; but it would be extreme to deny the intervention of olfactory stimulations. They are, however, not alone, and in certain cases one must perhaps also take tactile stimuli into account. However that may be, one is unable to affirm that the site of the nest coincides for the insect with this nest; and the recognition of the nest does not necessarily follow from the recognition of the path leading to the site.

From a general point of view the assemblage of well-established facts regarding the flying Hymenoptera permits a definite conclusion The orientation of these insects brings into play only sensory cues From the moment the insect starts in the direction of the nest, until that in which it arrives at the site of the nest, these cues are certainly and perhaps exclusively of a visual order

The manner in which these cues are registered seems complex Besides the fact that the cues are relations between objects rather than the objects themselves, it can be stated that the flying Hymenopteron registers at departure images linked together as they would be on return, since it flies off looking at the nest. But immediately after this, it registers images of which it must on return reverse the order of connection. Experimentation proves that this latter process is a matter of no difficulty, from its first excursion abroad, the insect retraces the path it has just travelled This result permits us also to say that the backward flight, executed by every Hymenopteron which leaves the nest for the first time, has perhaps no real utility.

As far as this is concerned, moreover, experiment furnishes reasons for thinking that it can just as well lead the insect into error, as facilitate its return. Experimenting for instance with the nest of *Vespa sylvestris* [35], I first of all arranged an exit by the bottom of the bell-jar; in a constant fashion the wasps which came out rose at once and flew above the bell-jar, having thus in view the upper part of the jar and its surroundings; in consequence, on returning they alighted on this part and never at the opening, which they took a certain time to find. Who, moreover, has not seen *Bombus* searching a long time in the neighbourhood of their nest before encountering it? Do not these hesitations arise precisely from the registration of images which do not exactly correspond with the nest site? Such hesitation is in vivid contrast with the assured flight of the Hymenopteron which follows the return path between the region in which it has been foraging and the site of the nest.

This path doubtless improves progressively and becomes simplified, various intermediate cues fade out and disappear; it is even probable that muscular memory is substituted for visual cues over a large part of the course. In all these cases, the visual cues immediately leading to the nest persist. It is these latter of which we have been able to grasp the co-ordination into a complex of superposed or successive planes. At the nest itself olfactory, tactile and perhaps other cues come into play.

To sum up, in the whole course of the path analysis finds sensory cues only; at no moment does it find occasion to adopt the idea of a special sense of any kind whatsoever

CHAPTER III

ORIENTATION IN WALKING INSECTS

DO these conclusions, which are valid for winged insects, apply to all the other Invertebrates? It cannot be admitted *a priori*, for the conditions differ essentially in the two cases. Assuming that the animal registers visual images, it naturally does not register them in the same way; and neither are they comparable images. Furthermore, the fact of walking brings the animal into immediate contact with various stimuli which are encountered by the flying insect only at the moment of alighting on the nest.

Among the Invertebrates which move about by means of walking, the ants have been by far the best studied, and it will be convenient to examine them first.

I.—THE ANTS

Like the winged Hymenoptera, the ants leave their nest, go a great distance, and then regain their point of departure, usually after having gathered booty of some kind.

When an ant goes out for the first time, or after displacement of the nest, the manner in which it behaves bears some analogy with the backward flight of bees and wasps. Admittedly, it does not leave backwards, but, having arrived at the opening, instead of launching straight forth, it stops and wavers, stepping to the right, to the left and forward, as if hesitating. The sum of facts actually known does not, however, oblige us to think that this behaviour, described by Brun[37], has any necessary relation to the recognition of the nest It does not, as we shall see, prevent very considerable hesitation on return, and perhaps it is the same with this attitude on departure as with the backward flight of bees However this may be, once the ant has come forth and is on its way, two very distinct cases have to be considered, according to whether the insects move about singly, or follow each other in column formation. Each case demands separate study

A.—Collective Journeys

When the ants move about in columns, they form often very long files, and follow worn paths, which are more or less numerous around a formicary, are always well-traced, and adhered to very exactly Observers have for a long while recognized that the ants using these paths are guided by the odour with which the latter are impregnated. Numerous facts support this opinion, while showing that though olfaction may play the principal part, it does not play an exclusive one.

Of all observers, Fabre [illegible] alone denies the intervention of the sense of smell. He finds, however, that red ants, leaving in a column, follow on return all the windings of the outward journey; but after having provoked a lengthy disturbance by sweeping the track, drenching it with water, impregnating it with mint, and covering it with paper or yellow sand, he concludes that ants proceeding in a column are guided by visual cues. Without further proof, he affirms that these cues are taken from microscopic objects, on a scale with the ants. He has, obviously, forgotten to make the necessary counter-experiment, either by blinding the ants or by removing their antennæ.[1]

The experiments of Forel [illegible], on the contrary, set the problem definitely.

Forel first removed some of the individuals from a collective track of *Formica pratensis* He cut off the antennæ of some, varnished the eyes and ocelli of others, and then replaced them on the path. The individuals without antennæ wandered indefinitely in all directions; they did not succeed in resuming the correct direction, and finally became lost As for the blinded individuals, although they manifested evident uneasiness, they nevertheless finished by taking the direction of the nest. At the outset they meandered somewhat, but this soon diminished, and the course became correct. On the outskirts of the nest, however, the insects went to a certain extent out of the way

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[1] It is to be noted, moreover, that after having admitted a "sense of direction" for the flying Hymenoptera, Fabre postulates sensory cues for the ants

Nevertheless for this species the suppression of the sense of smell took from the ant all possibility of returning to the nest, the suppression of sight induced only a passing and partial confusion. The *rôle* of olfactory cues seems then preponderant

This is also the case for other species, notably for *Formica rufa*, studied by Piéron[11] A column of this species was proceeding along a path strewn with rocks and stones By scraping with a rock over an extended surface, or by sweeping the ground, the author occasioned a marked disturbance He obtained the same result by altering the position of a stone or leaf on the trail, but the ants passed straight on when they met with this stone or leaf in its new position The interposition of an "odorous" obstacle caused equal uneasiness

We have all, moreover, been able to perform similar experiments, and to obtain concordant and very significant results.

In addition, it is right to emphasize that the *Formica* have relatively short sight, a fact that adds to these experiments an element of proof. If, in short, one is dealing with species which are blind or have poorly developed sight, olfaction alone enters into account. Forel states that an *Eciton* (blind)

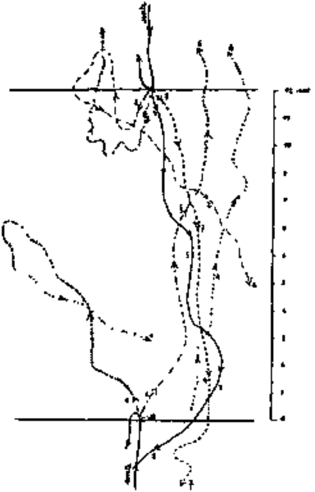

FIG 8.—Reconstruction of an olfactory trail of *Tapinoma erraticum* (after Cornetz).

which has been following a scent, resumes it without error on being turned aside. In the same connection, a *Polyergus* deprived of its antennæ is immediately lost.

Cornetz[31], for his part, has shown experimentally the way in which an olfactory trail is constituted. The necessary time for its establishment varies according to the species. It is particularly brief for species with a pronounced odour; such is notably the case with *Tapinoma erraticum*. If one cuts across a trail of ants of this species by sweeping it over a certain length, what will be the result? First of all a marked disturbance; the ants surge back in a mass from the two sides of the swept area. Then, at the end of three minutes some individuals begin to return, the first seven behaving in the following way (fig. 8). The first to arrive, moving rapidly, enters the swept zone, but, after going a distance of from 6 to 7 centimetres, stops confused and finally returns in the reverse direction. The second, arriving from the opposite side, advances a little, retires, and then returns and crosses the swept zone in a definitely oblique direction. The third, after a brief excursion at a slow pace, returns in the reverse direction. The fourth, after a definite return, decisively enters the swept area and crosses it slightly obliquely. The sixth and seventh cross almost direct, meanwhile describing wide curves. From this moment the trail seems re-established; for this to be effected, about eighteen minutes have been necessary.

The time, however, can be much longer. Cornetz counted one hour and twenty minutes at least for *Messor barbarus*. The nest being at *N* (fig. 9), some

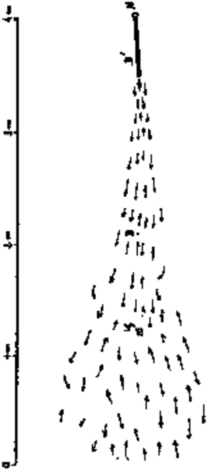

FIG. 9.—Reconstruction of an olfactory trail of *Messor barbarus* (after Cornetz)

seeds were placed at *G* before a worker which was 2.5 metres from *N*. During twenty minutes it journeyed back and forth, but without following exactly the same path; then other workers came out, followed the trail of the first for a length of 50 centimetres, as far as *D'* and dispersed beyond that point. The dispersion was very marked at *D*. Several arrived at the seeds, and at the end of about an hour and twenty minutes had traced a path from 3 to 4 centimetres wide. From this moment every ant placed on the path wandered for a longer or a shorter period, according to the distance at which it found itself from the nest, that is to say, according to whether the trail was more or less well defined.

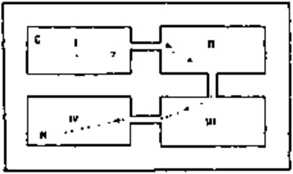

FIG. 10.—Formation of an olfactory trail (Santschi's experiment).

In a general way, once the path is established, the ants follow it regularly, so much so that at the end of a certain time, one sees visible traces on the ground, in the form of a linear depression.

How is this trail marked out? Is prolonged or renewed contact of the ants with the ground sufficient? Santschi found "that ants going afield (*Acantholepis frauenfeldi, Tapinoma erraticum, Camponotus maculatus*) emit a secretion which impregnates the ground. The following experiment demonstrates this clearly. In one of the compartments of an artificial nest (fig. 10) were enclosed twenty workers, which were kept without food for three days. On the third day, after some syrup had been placed in the fourth compartment, the passage was opened. An ant explored the three consecutive compartments, encountered the syrup, and returned dragging its abdomen on the floor. From this time the other ants followed the trail, and went directly to the syrup."[1]

No doubt remains as to the existence and utilization of an olfactory trail. One point, however, must detain us. When the trail is interrupted, after a short period of confusion it is finally re-established; this implies that the ants resume the same direction, following it in the absence of olfactory cues. What influence do they obey?

According to Cornetz, the ants would possess a general orientation to the way (*pure direction*), and follow it out on the disappearance of odorous trails. The term "pure direction" may lead to confusion by evoking the idea of a transcendent faculty. If I have properly understood the thought of the author, it is a question, in reality, of acquired orientation, of a sensory cue of a nature perhaps difficult to state precisely, but devoid of all mystical signification. We shall see later that Cornetz' interpretation corresponds probably with positive facts, and that the insect makes use on the return, of an "orientation" registered on the outward journey. It is, nevertheless, not the only factor intervening, and its action is not always predominant. Other cues enter into account according to the species, as well as to the circumstances.

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[1] Santschi speaks of a trail "intentionally" traced. It is not necessary to follow the eminent experimenter as far as this.

One fact, at the outset, should claim attention. When one removes an ant from its path, and replaces it a little later, it resumes the direction which it was previously following. In the impossibility of *seeing* the nest, by what cue does it guide itself? Does the olfactory trail furnish some sign or other which indicates the direction of the nest? Forel supposes that the ants possess a topochemical sense, and that they are capable of localizing their olfactory sensations in space. They would then perceive differences in the mode of emanation of odours, they would distinguish the "elongated smell of a blade of grass, the rounded and different smell of another leaf . . . that of a clod of earth . . . that of a passing insect, and so on." The ant would then not confuse its right with its left, and everything would take place as though, according to the expression of Bethe, the collective trail were *polarised*. Forel founds his conception on the fact that ants (*Formica pratensis*) captured on a trail leading to a group of aphides, then replaced on this trail a metre from the point of capture, resumed the direction they were following, after some very short circuits. This observation appears to him to correspond to an experiment made

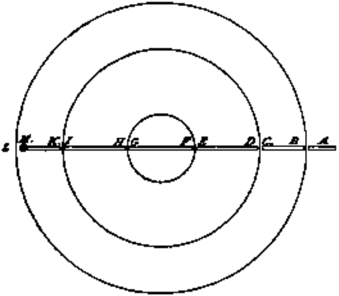


Fig. 11.—The concentric rings and movable disc of Lubbock

by Bethe[1]. A movable disc was introduced into a collective trail; when by successive journeys the ants had sufficiently marked the odorous trail, the disc was turned through 180°; the trail still existed, but the segment corresponding to the disc was exactly reversed. The ants manifested a very lively disturbance, going back and forth over the disc, greatly agitated It was only when their coming and going led them to the other side, that they resumed their route tranquilly, either towards the nest or towards the aphides.

Though evidently very ingenious, Forel's conception certainly does not account for the facts. If it is true that an ant displaced on a collective trail resumes the same direction, this result is not due with certainty to a difference recognizable by the insect between the right and left sides Bethe's experiment permits another interpretation. In fact, a previous experiment by Sir John Lubbock, undertaken with quite a different aim, does not give at all the result indicated by Bethe Working with *Lasius niger*, Lubbock took two concentric rings and a central disc, movable on one another (fig. 11), in such a way that they could rotate independently. Now, when he turned through 180° either *LA* or *GF*, while leaving the ring *IG* fixed, he observed no modification in the movements of the ants ; they continued straight on their way.

One or several other conditions, then, intervene. One of these conditions is due to the fact, according to Brun, that the odour of the trail diminishes progressively in intensity as the nest is left ; this gradual diminution he thinks would guide the ant when going and coming. The fact would be particularly marked on trails leading from the nest to a group of aphides, and appreciably less distinct in other cases. In the former case, the general direction of the journey would be furnished by sight to ants stopped by a break in the continuity. Various experiments of Santschi establish this in a positive way. Here, for example (fig. 12), is a nest *N*, from which lead two trails: one in a direction from east to west (*a*), the other in a south-westerly direction (*b*).

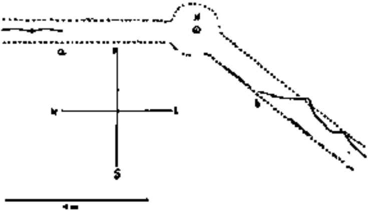


FIG. 12.—Influence of light on ants following an olfactory trail (Santschi's experiment).

From the trail *a*, an ant proceeding towards *N* is removed and placed on trail *b*. It continues its journey towards the east, and goes off the trail; but is immediately led back to it by the odour. A little afterwards, notwithstanding, it again takes the direction of the east, and again the odour leads it back.

Brun obtained the same result and arrived at the same interpretation by a different experiment. Over an ant which was going away from the nest *N* towards the sun, at three p.m. (fig. 13), Brun placed a box, enclosing it thus until five p.m. He then raised the box and the ant departed, retracing its steps in the opposite direction from the sun. Brun noted that the angular difference between the outer and return journeys corresponded to the angle formed by the positions *S* and *S'* of the sun before and after the imprisonment of the ant.

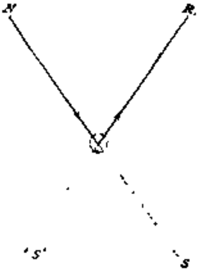


FIG. 13.—Influence of light on ants (Brun's experiment).

These experiments doubtless do not exclude the hypothesis advanced by Cornetz of an orientation in general direction. But as Santschi, and after him Brun, have established with certitude, as we shall see, the *rôle* of luminous cues, there is ground for assuming that these cues intervene in the case of partial destruction of an olfactory trail. As a consequence, we find ourselves led to think that ants going over a given trail register *at least* two orders of cues, one visual, the other olfactory; the one or the other predominates according to species and circumstances. Species with good sight and feeble sense of smell, such as *Cataglyphis*, use especially visual cues, and are able to continue their route after removal of the antennæ; short-sighted species utilize rather olfactory cues, and are more or less disoriented by amputation of the antennæ, as is *Messor*. Within a given species, one or other of these two senses comes into play in virtue of the age of the trail. The older this is, the more odorous, and the less sight intervenes; this, however, plays the principal part at the commencement of establishment of a trail, or if by chance it is interrupted.

Tactile cues intervene as accessories. Turner[88] shows that the interposition in a path of a velvet surface is sufficient to confuse the ants. These varied stimuli are associated with, complete, or replace one another, and these multiple interferences show all the complexity of the process.

B.—Isolated Ants

We shall perceive this complexity still more when we enter into the facts in detail by studying ants which leave the nest alone, without following a beaten track. Olfaction is, in consequence, eliminated, except on arrival, and this circumstance permits us to proceed to a more precise examination of other cues

The ant which moves about alone sets out at hazard After having travelled about for a certain time, having fed or gathered booty, it returns towards the nest For it, as for flying Hymenoptera, a distinction must be made between the return in general direction and the recognition of the nest site

This appears to coincide with the recognition of the nest itself. The analysis of the process presents no difficulty, and it is preferable to examine it forthwith, in order not to have to return to it.

a. Recognition of the nest site. When, following a general direction, the ant arrives at the level of the nest, it does not necessarily happen on the nest itself, but only on the immediate zone, sometimes barely a few centimetres away One sees it then go hither and thither, describing twists and turns, well observed by Turner[54] in a dozen species, it performs, in a word, the turning which Cornetz terms "*le tournoiement de Turner*" This is caused by the multiplicity of individual olfactory trails which intersect in the neighbourhood of the nest. As soon as the ant encounters a collective trail, from which doubtless emanates a stronger odour, it goes straight to the nest. The turning lasts less long in species with good sight which utilize other cues, than in species with feeble sight for which olfaction plays the chief part For both alike, everything masking the cues, for example the carrying of booty sufficiently bulky to limit the functioning of the antennæ while also obstructing sight, increases the uncertainty.

This takes place only in the immediate surroundings of the nest. Up to that point, the insect follows independently of all olfactory trails, a general direction which leads it exactly to these immediate surroundings. What cues does it follow? To what influences is it subjected?

b. Progression in general direction. At the outset, an essential statement is imposed: *the outward journey conditions the return.* All present writers, Cornetz, Santschi and Brun among others, are unanimous and precise. From this point of view, then, the ants behave like the flying Hymenoptera. Ants *carried* away from the nest either do not find it again, or if they do so, it is only after having wandered more or less at length, turning more or less regularly. The return to the nest depends in this instance on pure chance, and nothing distinguishes ants from bees and wasps in this respect.

But, on the other hand, every ant which has gone away from the nest on its own account returns to it, even if large distances are traversed; the return path is parallel to the outward one, whatever may be the complexity of the latter. Cornetz[16] was the first to establish the fact of this parallelism, which has been confirmed by Santschi[81]. Most often (in 90% of the cases), the ant which travels away from the nest follows a single direction. Its progress is not strictly rectilinear; it is cut into by "explorations" (fig. 14, *E*), but after a short or prolonged

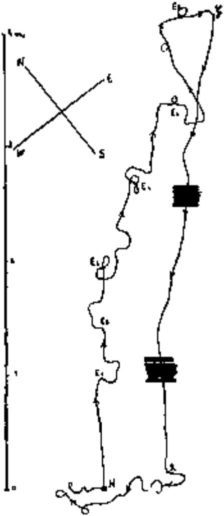


Fig. 14.—Outward path in single direction (*NG*), and return path (*GN*), of an isolated ant E_1, E_2, E_3, etc., explorations (after Cornetz).

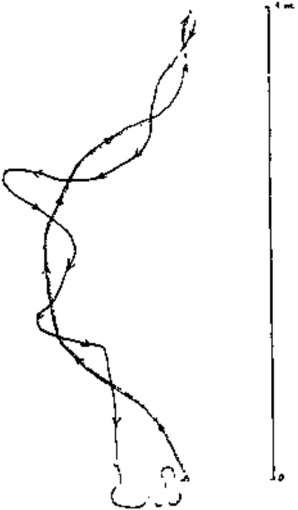


FIG 15.—Outward path in two principal directions (line doubled by dotted line), and return path of an isolated ant (after Cornetz).

curve, the insect resumes its original direction. As soon as the ant encounters an attractive object, it takes this in its mandibles, turns through 180°, and sets off towards the nest. In this also, the ant behaves as does the bee which has just found booty. From the moment it resumes the direction of the nest, it follows a perceptibly straight path, 40 or 50 centimetres distant from the outward path. At the level of the nest it stops, and there the turning commences.

In some instances (fig. 15), the ant follows on the outward journey two directions, usually at right angles; the return is none the less parallel, sometimes cutting across the outward path. Finally, in exceptional cases the ant adopts three directions which it adheres to on return, even if the point stopped at is relatively near the nest (fig. 16). In the two last-mentioned circumstances, however, it happens that the ant takes the shortest cut; we shall examine this particular case later. Under all conditions, the ant stops at the level of the nest, even if the return path leads it laterally for some distance.

The problem being thus clearly stated, the question arises as to what are the factors determining the return. Olfaction does not enter into play, since neither sweeping nor obstacles turn the ant from the path. The experiments of Cornetz are decisive on this point: the sweeping of a broom in front of the returning insect (fig. 14, *B*), remains without effect. In addition, the ant sometimes cuts across the outward path, and is not retained by it. The

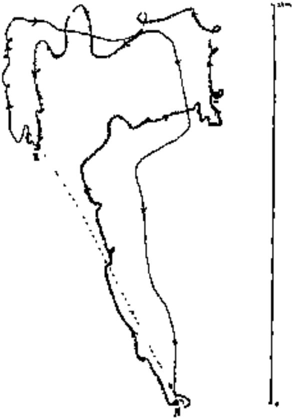


FIG 16.—Outward path in three principal directions (line doubled by dotted line), and return path of an isolated ant N, nest, R, commencement of return. The dotted line NR indicates the straight line leading to the nest, which the ant does not take

insect follows a new road which cannot yet be impregnated with any odour. Three questions, therefore, must claim our attention: the resuming of the general direction after encounter with booty, the

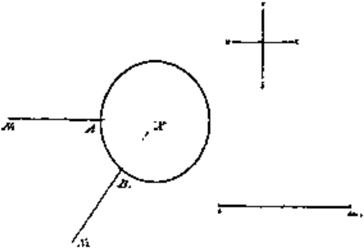


FIG 17.—Nest with two openings, N_1, N_2. X, piece of bone placed under a cover. The ants which emerge from N_1 go under the cover at the point A; those which emerge from N_2 enter at the point B.

return by a parallel route, and the halt in the region of the nest, and at the level of the latter.

The first question formulates itself here in the same way as in the case of the flying Hymenoptera, but the ants furnish some elements which permit us to foresee a solution.

There exist, in fact, ants which go abroad at night, or at the least in badly-lighted places. Many of them, moving about alone, do not make use of any olfactory trail. Now, after having circulated about, they take again the direction of the nest. An experiment by Cornetz[illegible] is very suggestive on this point. In proximity to, and to the east of a nest of *Tapinoma erraticum* having two entrances N_1, N_2, the experimenter deposited in the twilight a bone over which he placed

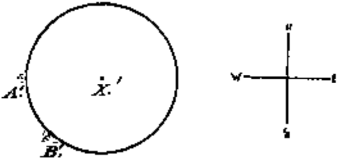


FIG. 18.—A', B', points at which the ants stream out from the cover (after Cornetz)

a cover (fig. 17). The bone was soon discovered by the ants, which passed under the cover equally from N_1 and N_2; they thus followed two directions: from west to east, and from south to east. The bone, extensively attacked by the ants, was transported at night 5 metres to the north, hidden under the cover to avoid all influence of light, however feeble. In addition, it was placed down after rotation through 90°. Half an hour later, the ants commenced to leave the bone, coming out from under the cover by the points *A'* and B' corresponding with *A* and *B* (fig. 18), then following two directions from east to west and from south to west, that is to say, two directions parallel to those followed on entering (fig 19).

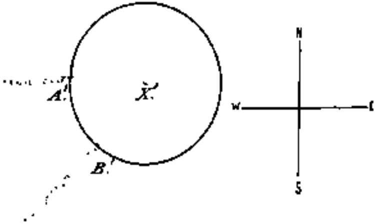


Fig 19.—The ants outside the cover follow two directions parallel to AA_1, and BB_1 of fig 17 (after Cornetz)

The experiment, which was repeated several times, seems to have been conducted with all necessary rigour, and should be held valid. Without doubt, as Santschi[illegible] remarks, the observer does not see what takes place under the cover, and there is nothing to prove that all the ants resume at the outset the direction taken on entering; there may perhaps also exist a slight deviation between the entering and return journeys; the general direction is none the less taken, and that alone is of importance.

Now, under these circumstances the ants make no use of olfactory, visual, or tactile cues; they were on the bone at the moment of transportation; they were deposited in new territory where there could exist no trail parallel to the two initial directions; they had been transported at night, not only to a considerable distance, but into an appreciably different environment. We are constrained to admit, until proof to the contrary, that the ants registered a certain direction. Evidently they could do so only by reference to the bone, for it must be emphasized that they register the direction of active change of position and never of passive removal. The transport of the bone 5 metres to the north of its original position certainly exercised no influence on the return reaction. There is no question then of a mysterious and inexplicable inner sense, of a sense of "attitudes", nor of anything resembling it, but of a direction taken in relation to an exterior cue. Such is at least, the significance which to my mind emerges from Cornetz' experiment. The cue, in this case, can be only the bone.

The latter undeniably underwent a rotation of 90°; but need great importance be attached to this rotation? The ants probably circulated to a certain extent in all directions on the bone, and the change in orientation imposed on it adds hardly at all to the effect of the comings and goings of the insects, especially as it was a passive change in orientation. To suppose, then, that the ants register the angles thus described amounts to formulating an entirely gratuitous hypothesis. As a matter of fact, every ant which abandons the bone and resumes the direction of entry, behaves in the same way as the one which meets with a booty and returns along the road to the nest—and in the same way as every flying Hymenopteron which executes the same movement in analogous conditions. The experiment of Cornetz, by eliminating a series of variables, indicates that this turning round is not necessarily directed by the habitual exterior cues. In all probability, the cue is the actual object encountered by the insect, whether it carries it away or abandons it.

What is the connection which is thus established in the nerve centres of the insect between this cue and the outward direction? We are quite incapable of saying what it is. The fact remains, and is moreover not isolated, so that it should not be needful to consider the establishment of such a connection as necessarily bound up with the process of return to the nest.

Cornetz' experiment is in fact in close agreement with experiments which I myself carried out independently, and of which the first dates back to a period when, by reason of circumstances, I had not become acquainted with the work of Cornetz. At that time I observed the relation of these experiments to the problem of orientation, and it now appears to me extremely close.

It was in September, 1916. I encountered on a path a caterpillar of *Cossus ligniperda* coming from a neighbouring willow and going towards the east. With the end of a stick, I turned it aside; but it immediately resumed its direction. Successive attempts remained entirely in vain Whether I caused it to perform a rotation of 30° or of 180°, once it was left to itself the caterpillar executed a rotation in the reverse direction of approximately equal value. If I placed an obstacle in front of it, it skirted round this without allowing itself to be diverted Finally, I permitted it to advance along the path; it entered the bordering ground, traversed a distance of thirty metres (in twenty-five minutes), coming into contact with various herbaceous tufts, and at length stopped at one of them and began to burrow I straightway extracted it and carried it to the point of departure; scarcely liberated, it set out again, once more towards the east. I interrupted the experiment and imprisoned the caterpillar in a flask Two hours later, I liberated it at the exact spot at which I had come across it. This time it took a northerly direction, and arrived at the foot of a wall. Led—or *thrown*—back several times to its point of departure, it returned always towards the north.

In the course of experiments, I established the fact that the dryness or humidity of the soil plays no part in the phenomenon By moistening at certain points the ground over which the caterpillar was moving, I induced no appreciable reaction. Encounter with a tract of ground strewn with débris of straw or grass produced a more noticeable effect; the caterpillar was not attracted to, but retained by it. Taking account of this fact, I transported the animal to the western edge of the path, placing it in contact with grasses and straw. Immediately, abandoning the northern direction, it proceeded towards the west. From this time onward, as often as I carried it back to the middle of the path, it started invariably towards the west, in spite of all my efforts. In short, as I have noted above, everything took place as if the animal starting in any given direction found itself, by virtue of this fact, *polarised*.

I have since repeated the same experiment with caterpillars of *Bombyx rubi* met with on the roads, and have constantly obtained analogous results. By guiding the caterpillars with the end of a stick, one succeeds in turning them aside, but immediately they are left to themselves they resume the original direction.

Finally, I quite recently worked in the laboratory with a scorpion (*Buthus occitanus*), under more rigorous conditions The results agree with the preceding ones. The Arachnid was placed at one of the extremities of a long table, the room being lighted by two powerful lamps, one on each side. The animal set off in a certain direction; led back to the point of departure, it persistently resumed that direction The two lamps were extinguished alternately without modifying the result. It was only after having caused the scorpion to effect a forced journey by guiding it with a stylet that I succeeded in making it take the reverse direction. What was the cue by reference to which the scorpion changed position? Perhaps it was the edge of a cloth turned back on the half of the table; in any case, it was not a luminous cue. The principal interest of these experiments with caterpillars or scorpions is that these animals, so persistent in moving in a given direction, are not subject to any attraction comparable with that which might be considered to animate a nest-building Hymenopteron. We have to do with a process which seems very widespread, and which corresponds very probably to the registration of a cue imposing a certain direction on the animal, whether or not this direction leads back to the point of departure.

To return more precisely to the ants, it is needful to state that the resumption of the general direction, in spite of its importance, is, however, not all that is involved. Thus "general direction" is not necessarily that of each of the sections of the journey, and, when the outward course is effected by following several directions perpendicular to one another, the ant takes on reversing at the moment of return, the direction of the last section of the outward journey, which does not of necessity coincide with the direction of the nest.

Must one admit for the ant which moves from place to place a "sense of described angles", more or less comparable with the "sense of attitudes"? This hypothesis, advanced by Cornetz and Santschi, is not based on any positive fact. Undoubtedly, when an ant mounts a movable disc, which is then rotated through 90°, the insect executes a rotation of the same amount in the reverse direction. But that in no way demonstrates the existence of a sense of described angles. We shall see later that the retaking of the direction depends on a cue external to the ant, often on a luminous cue. The hypothesis cannot be retained.

Must one think of muscular memory, and consider that the insect returning in the general direction estimates the distance to be traversed, and after having travelled a certain length, stops approximately in the region of the nest, and at its level? Kinæsthesis would explain equally the parallel return and the halt at the nest.

The hypothesis, as a matter of fact, is founded on actual observation and on experiment. The observation deals with the parallelism of the return journey in relation to the outward one, a parallelism which is sufficiently rigorous on the whole, even for short-sighted species such as *Messor*. To this established fact is added the classical experiment of Piéron [47]. Suppose a *Messor barbarus* is going towards its nest at a slow pace. Before it (fig. 20) let us place a piece of paper covered with earth;

once the *Messor* has embarked on this movable platform let us displace it laterally several centimetres. The *Messor* continues its journey, and, when it has covered a distance equivalent to that which separated it from the nest at the moment of lateral displacement, it stops, manifesting at times a certain hesitation. Similarly, if we transport the movable platform beyond the nest, in a symmetrical position, the *Messor* proceeds further away from the nest, and halts at a corresponding distance to that which separated it from the entrance at the moment of removal.

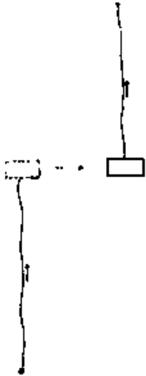


FIG. 20.—Scheme of Piéron's experiment: the ant, captured on a sheet of paper, is transported some distance (following the direction of the arrows).

It would seem that the conditions of the experiment exclude olfactory and tactile cues, since the ant finds itself on new ground, but they do not necessarily exclude visual ones. The experiment does not always succeed with ants which move rapidly and have good sight, *Formica cinerea* for instance. With them, transporting occasions a violent agitation. Nevertheless, it is proved that washing the ground and the interposition of obstacles fail to turn these same ants from the track, a fact which forbids the suggestion of smell or touch. Amputation of the antennæ and varnishing of the eyes, however, cause immobility, a result which cannot be entirely neglected.

The positive result of Piéron's experiment nevertheless remains. It has received confirmation from Cornetz[illegible], with this additional information that the progress is slower, more hesitating and more winding after transport. Santschi, also, has observed similar facts, and he too admits the existence in ants of an "estimation of distance". He has, however, not always obtained concordant results. In certain instances, the transported ant halts after having gone half the distance it would normally have travelled According to Santschi, it is not a question of a memory for attitude, since the return is carried out often with a burden which involves different attitudes from those involved on an unencumbered journey. He admits, though, that *previous returns* leave a memory of effort accomplished and of distance covered in *known territory* To muscular effort are then added cues of another order In addition the experiment of lateral or symmetrical transportation does not succeed with blind ants; neither does it succeed with those endowed with sight when the use of light cues is impossible. Brun further proves that the experiment fails when the transportation places the ants on *dissimilar territory*.

From this mass of experimental data it emerges clearly that kinæsthesis does not under the circumstances play the predominant *rôle* In all probability, for the ants, as for flying Hymenoptera, kinæsthesis is established secondarily in the course of several journeys back and forth; it is a process of substitution and not a process of immediate registration of cues The question is certainly more complex; other cues come into play.

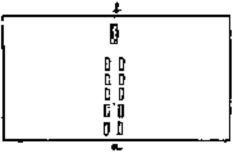


FIG 21 —Lubbock's arrangement for the analysis of the cues guiding ants

The influence of light cues was long ago invoked by Lubbock, who brought it into evidence by means of two series of experiments The first consisted in making use of a movable board on which some ants (*Lasius niger*), were induced to walk about. On the board a tunnel was arranged (fig 21, *b*), under which the insects passed; two rows of wooden blocks lined a path at the end of which food was placed (a). Once the way was known, the arrangement was altered, the board retaining the same direction (fig. 22). The ants no longer went under the tunnel, nor between the double row of blocks, but pursued the same direction as before relative to the board. Repeated several times under diverse forms, notably after removal of the tunnel (figs. 23, 24), the experiment gave the same result. The displacement of material cues did not modify the course of the ants; they went always to the same point on the board. It was not then the immediately surrounding objects, the tunnel and blocks—objects on a scale with the ants—which guided them. But it may have been an olfactory trail, for the insects constantly passed over the same road. In order to test this last hypothesis it was sufficient to move the board, when it was proved that the ants still took the same

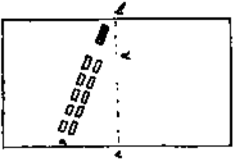
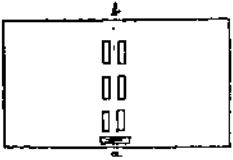


FIG 22.—b, d, e, direction followed by the ants when the tunnel and blocks are moved

direction, entering on a path that they had not hitherto followed.

The second series of experiments carries with it a much greater precision. Lubbock used a disc composed of two concentric rings, each turning

FIG 23.—*ba*, the line followed by the ants when the tunnel is removed, the blocks remaining in place



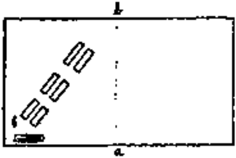


FIG 24.—*ba*, the line followed by the ants when the tunnel is removed and the blocks displaced

independently around an equally movable central disc (see fig 11, p. 54), and placed it beside an ant-nest; he deposited a repast at *B*, in such a way that the ants were induced to come and go following the line *AB*. Whilst an ant going towards *A* was between *E* and *D*, the ring *ED* was turned through

180°; the insect performed a rotation of equal value in the reverse direction; then it resumed its journey towards *A*. What factors determined this rotation? Did the trail marked out come into play, or the correction of the angle described?

Let us recommence the experiment, covering the arrangement with a box, simply pierced on top by a hole which permits observation of the ants. We establish the fact that 19 out of 30 individuals do not rectify the rotation effected whilst they are under the box; they continue on their way, returning thus towards the point of departure. The introduction of the box into the arrangement of the experiment plays, then, an important part Manifestly, the odorous trail does not suffice to lead the ant back in the right direction, and one cannot really speak of the angle described.

Lubbock then formulated the hypothesis that the light guides the ants In consequence, he added two candles to the arrangement. If, under these conditions, he turned the ring on which the ants happened to be, while moving the candles in the same direction, the insects did not compensate for the angle described, but continued their journey in the reverse direction; but if he turned the ring without moving the candles, the insects rectified the direction, setting out once more towards the same point. Finally, if he moved the candles while leaving the apparatus entirely stationary, five ants out of seven went the wrong way.

From these experiments the part played by luminous cues appears clear enough. However, as they were performed only with a single species, they are not sufficient.

Viehmeyer[29] has confirmed them by study of another species, *Leptothorax unifasciatus*. Some individuals of this species had established their nest in a glass jar placed near a window. The nest at first occupied a central position The ants next established another on the side away from the window. While they were going from one to the other, changing the quarters of their larvæ, the jar was rotated through 90°; the ants, confused, followed a direction which led them away from the window, and heaped their larvæ in a part of the jar where there was nothing. Were they repulsed by the light, and not merely guided by it? To settle this point, Viehmeyer installed a light on the opposite side from the second nest, and placed food beside it Once the habit was formed, he moved the light without touching the food, and proved that the ants modified their direction by following the displacement of the light

Working with 12 species, Turner arrived at concordant results Above an artificial nest, he arranged a platform connected with the nest by two strips of cardboard; beside one of these he installed an electric light. On the platform he placed a handful of ants and cocoons; the ants soon discovered the strip of cardboard next to the lamp; they came and went along it, carrying the cocoons to the nest The lamp was then moved; the ants, disturbed, took to the other strip. The movements of the

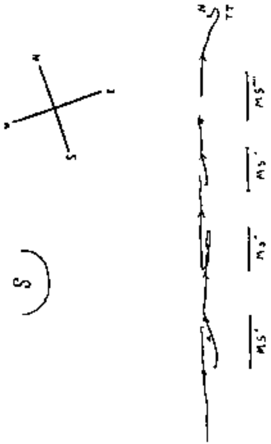


FIG 24.—Influence of solar light on the direction taken by ants MS', MS'', MS''', MS'''', action of the mirror; TT, final turning N, nest The action of the mirror is weakened as the nest is approached (after Santschi)

insects were thus connected with the positions of the electric lamp

The phenomenon appears to be sufficiently general.

It is however connected with laboratory experiments, and it may be asked if they have any equivalent in nature. The idea that the sun might guide ants which move about in broad daylight should be entertained. But how can this be put to the test? Santschi[28] performed, in this connection, the crucial experiment. Utilizing ants (various *Messor* and *Myrmecocystus*) which were returning to the nest, he interposed a screen between them and the sun, and then displaced the solar light symmetrically by means of a mirror (fig. 25). Under these conditions, the ants wheeled through 180°, and went in the opposite direction; they resumed their original direction as soon as the mirror was removed. In a general way, the deviation was proportional to that of the light rays; but it was less marked as the ant, approaching the nest, picked up collective odorous trails. These trails absorbed the insects, over which thenceforth the influence of the light was exercised with more feeble intensity.

Other disturbing influences enter moreover into play, notably a very strong wind. In addition, the sun hardly ever acts singly, large well-lighted neighbouring objects serve equally as cues. The following experiment gives a precise example of this fact. A *Messor barbarus* is proceeding towards its nest; in front it has the sun, to its right a row of sheaves for a distance of ten metres (fig. 26). When placed on the left, the mirror provokes a deviation of only short duration and slight width, a matter of twenty centimetres, when the ant resumes its course without further deviation, in spite of the continued action of the mirror. When placed, on the contrary, between the row of sheaves and the ant, the mirror occasions a marked and lasting deviation. Evidently the row of sheaves, vividly

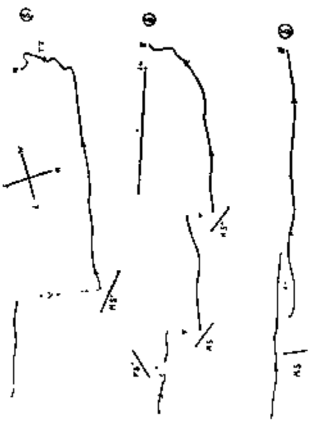


FIG 26.—Action of solar light on the direction of ants, and interfering influences (after Santschi) MS′, MS″, action of mirror. N, nest. TT, final turning (The effect of the interfering influence is indicated on the middle path as MS′.)

lighted, serves concurrently with the sun as a guide to the *Messor* The sun's influence, however, seems undoubted. It can thus be very well explained how it is that ants following a collective trail continue on their way after destruction of the latter In addition to the olfactory cue which guides them, they register a luminous cue, which comes into play when the former fails. Isolated ants receive olfactory cues only in the immediate neighbourhood of the nest; visual cues direct them during their return journey

The intensity of illumination, furthermore, should enter into the reckoning Even when filtering through clouds or trees, the sun would perform the office of guide by the simple effect of unequal radiance. It suffices for the direction of the rays not to be perpendicular. If the sun is at the zenith, it obviously gives no direction to an ant moving along a horizontal plane.

By way of counter-experiment, Santschi demonstrated that ants with daylight habits are completely disoriented when the light is suppressed. An ant going towards its nest was covered very gently by a basin measuring 40 centimetres in diameter and 30 centimetres in height, perforated at the base by an opening of 4 centimetres. Confused, this ant turned in a circle on itself, finishing by attaining the edge of the basin, then by getting out; once outside, it continued its direction. Does the confusion result simply from the action of the basin in serving as a closed vessel, or from all the other causes due to the presence of the basin? But if the ant is covered with a bell-jar, no disturbance is provoked, under this, it persists in its direction.

An objection nevertheless suggests itself. The relative position of the sun changes, and in such a way that the ants could be led in the opposite direction from their course Now, observation shows that many ants such as *Polyergus* go out at fixed times, and their absence lasts a comparatively short period, so that the relative positions of the sun on departure and return are not essentially different. Deviations, furthermore, are not at all rare, and one may count a number of strayed individuals. Brun's experiment, reported above, shows exactly how the change in position of the sun induces a change of direction (see fig. 13, p. 57).

It can then be held as certain that the sun serves as a guide to ants moving about in full daylight. But there are some which, even though possessed of eyes, go out only in the evening. What then are their cues? Santschi is of the opinion that they are luminous ones, the moon or the stars, or that obscure radiations are perceived. He bases these hypotheses on the following experimental data:

A *Myrmecocystus bicolor* was returning towards its nest at 8 p.m., "after the sun had set, carrying booty. 15 metres from the nest the antennæ were cut off. The dropped booty was not recovered; the insect wandered about, finally departing towards the nest, walking straight ahead in spite of the darkness."

Several analogous experiments give the same result. If, by way of counter-experiment, the eyes are varnished while leaving the antennæ intact, it is found that there is a lengthy wandering, much more prolonged than if the antennæ are cut and the eyes left free; and if the antennæ of these blinded ants are cut off, there is occasioned either immobility or rotation in one place.

The *rôle* of sight then seems hardly to be disputed. Nevertheless, one cannot assume in this case the hypothesis of obscure radiations or of sidereal cues. Without calling on such an hypothesis, it is sufficient to state that night does not exclude the possibility of objects as visual cues, a fact brought into evidence by Santschi for ants moving about during the day.[1]

Whether it is a question of diurnal or nocturnal ants, it must be asked how these cues are utilized. The facts already known permit us to estimate this to a certain extent.

Cornetz, for example, captured a *Myrmecocystus* on the confines of the nest, and transported it to *D* (fig. 27). As soon as it was on the ground, the ant started off, walking with rapidity, and describing various loops. Suddenly, at C_1, it took the direction of the nest, proceeding in a straight line. It was captured afresh at P_1, at the moment of arrival at the nest, and placed down at I_1, on the very track which it had just traversed from C_1. It set off at

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[1] A number of nocturnal ants follow especially collective paths, and this is the rule for blind ants

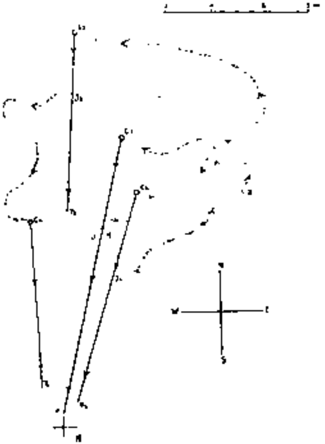

Fig 27.—Utilisation of sensory cues N, nest, P_1, P_2, P_3, P_4, points at which the ant was captured, D, I_1, I_2, I_3, points where set at liberty, C_1, C_2, C_3, C_4, points where the direction of the nest was taken [after Cornetz]

hazard, describing zigzags away from the nest, then, arrived at C_2, turned suddenly about and advanced towards the nest. The experiment was performed a second time; captured at P_2 and set down at I_2 on the path it had just been traversing, the ant moved away from the nest making a wide circuit and, having arrived at C_2, took the straight line towards the nest. Captured a third time, at P_3, and released at I_3, on the line it was following, it moved on without fixed direction until the moment when, arrived at C_3, it set out plainly in the direction of the nest.

Thus all occurs as though the ant registered various cues in the region inhabited by it. These "known places" are naturally much more numerous as the nest is more nearly approached. Cornetz thinks that they constitute so many *isolated* cues, which are associated with the previously taken direction. The sum of acquired facts, for the ants as well as for the flying Hymenoptera, calls rather for another interpretation.

Though it is probable that an ant, actively moving from one place to another, registers a certain direction, this is a relation registered in regard to a certain cue; it will with difficulty be accepted that the direction exists independently, and that an ant *transported* separately retains this direction. In all probability, the cues are not thus registered in isolation but in relation to one another and to the nest; as they are consecutively connected in a certain manner, encounter with one of them suffices to evoke the succeeding ones.

Such is, moreover, the opinion of Brun. He observed that ants captured at the nest and carried no matter where, often knew where they were immediately; others at first turned about and sometimes ended by finding themselves. They behave, then, in opposite ways under similar circumstances where, having undergone passive transport, they have been unable to register the least direction. This observation suffices to eliminate the hypothesis of the registration of a "pure direction". External cues alone intervene.

Putting on one side the sun, whose indubitable *rôle* is nevertheless not exclusive, what then are these cues? An experiment of Santschi, previously reported (page 82), leads us to think that the ants register the image, not of small objects on their own scale, but of large ones, such as a row of sheaves. This observation finds confirmation in a series of others by the same author.

A *Messor barbarus* inhabited a nest two metres to the south of a large wall; transported parallel to the wall, in a southerly direction, it manifested no confusion in orientation. But if carried ten metres from there to the north of another wall, it was disoriented and often lost. The first wall played then, very probably, the part of a fixed and constant cue.

A nest of *Camponotus maculatus* was situated at the foot of a date-palm. If some individuals were carried two or three metres away from the palm, they returned always without hesitation; but they showed momentary disorientation on descending to the bottom of a furrow, which decidedly hid the tree from view.

Santschi, furthermore, established that the mirror experiment succeeded indifferently, as in the case of the sheaves, when performed in a courtyard or near a wall.

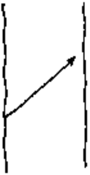

FIG. 28.—Transfer of an ant from the left to the right column

To these facts Brun adds others no less significant. Two columns, *A* and *B*, of ants (*Formica rufa*) proceeded parallel for a distance of 4 metres (fig. 28). An individual carried from *A* to *B* turned immediately towards *A* and resumed its original orientation. Now one is unable to invoke here the kinesthetic sense, since the ant had been carried; nor smell, since the two columns belonged to the same formicary; nor lighting, which was the same; nor any unknown sense whatever, since the direction did not change; one is forced then to admit distant visual cues which differed for each of the two columns by reason of the distance separating them.

The same conclusion emerges from experiments which consisted in directing the course of an ant, provoking what Brun calls a *forced journey* (*marche forcée*). With a straw or the finger, Brun chased an ant from the nest, and obliged it to follow a certain path. When the path was simple, comprising a single direction for a length of from 5 to 10 metres, the ant, as soon as it was set free, started back towards its nest in *the most direct line.* If the path was rectangular, for a length of 17 metres in two directions, the return was promptly effected by the hypotenuse; the point to which it was led by forced progress was, moreover, not known to the ant, since, if transported there passively it did not re-find its way.

Does the ant register an image of the "polygon" described and of the compensation to be effected? This would be to ascribe to the insect the capacity to solve an arid problem of planimetry, and one should think rather of visual re-orientation by some large object

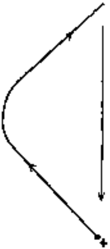

Fig 29.—Return of an ant after displacement on a forced journey

By varying the experiment on forced progression more precise information is obtained on this point. Let us oblige an ant to follow an angular track, 34 metres long, on which there is a tree at *A* (fig. 30); as soon as the ant is released, it turns back; but instead of taking the hypotenuse as in the preceding case, it first follows a return track parallel to the outward one as far as the point *A*. Arrived there it abandons the direction of the outward path, and, cutting the shortest way, takes the hypotenuse. There is no doubt here that the tree is a landmark definitely associated with the position of the nest

By way of control, Brun provoked forced progression in ants blinded by varnish, or in short-sighted ants. Liberated, the first did not return; as for the second (*Lasius niger*, *Myrmica laevinodis*), their returns were lacking in precision, having a lateral displacement reaching up to 30° for rectilinear outward journeys; for angular paths, the return, at first diagonal, tended to become parallel; it terminated in excentric turning. *Lasius niger*, whose eyes possess about 180 facets, arrived at length; *Myrmica laevinodis* (105 to 115 facets) turned indefinitely.

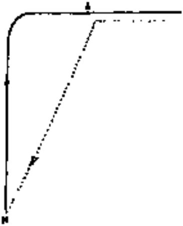

FIG. 30.—Return of an ant after displacement on a forced journey. *A*, a tree; N, nest

If, for ants with small eyes, large objects do not play a part of the first order in the conditions of the experiment, they are essential for ants possessing well-developed eyes. Cues of another order enter in also, notably the slope of the ground. Brun shows this by the following experiment effected with *Formica rufa*, whose sense of smell is very reduced.

The nest was arranged on a table, at the centre of which was some honey; the table was then inclined 20° towards the nest. While the ants were at the honey, the inclination was reversed, in such a way that the nest was at the top of the slope; on leaving the honey the ants displayed a slight hesitation, then *descended* in the opposite direction from the nest.

Thus, as far as the ants are concerned, orientation is effected by means of a complex of multiple elements, some or others predominating according to circumstances. Olfactory cues predominate for individuals proceeding in columns, but visual cues intervene when the trail happens to be accidentally destroyed. As for isolated ants, they follow simultaneously visual cues of various kinds—light and large objects—closely associated, and connected in addition with features of the ground, notably with the slope. Every cue is associated with all the others, but also with the topographical position of the nest, so that in the absence of any one among them, the others constitute a sufficient guide. These cues, however, are not linked in the memory of the ant in such a way that it need be obliged to pass from one to the other. For the ant, the road is not lined with a series of successive steps, so closely bound together that one evokes necessarily and exclusively the next. As in the case of the flying Hymenoptera, all takes place as if the ant registered a whole, in complete relation with the position of the nest, and registered in such a way that it is able on return to neglect zigzags and take the shortest route. In the long run, the return perhaps becomes a matter of kinæsthesis and appreciation of distance, at least from a determined point, and at a given distance from the nest.

Without a doubt, in all cases, the ordinary sensory cues are the sole factors entering into account The explanation of the return to the nest in no way leads us to assume the existence of any unknown sense, which would merit the name of sense of orientation. Experimentation gives evidence solely of a special process such that the insect takes the reverse, independently of visual, olfactory or tactile cues, of the direction followed on the outward journey. Certainly it indeed seems as though it actually registered a "direction", but it registers it, according to all probability, by reference to the object on which, or before which, it finds itself. This registration, moreover, does not seem peculiar to nest-building and social insects.

CHAPTER IV

ORIENTATION IN OTHER INVERTEBRATES

THESE conclusions, common for flying and walking insects, extend equally to all Invertebrates on which experimentation has been possible.

1.—TERMITES

The termites, notably *Eutermes monoceros*, studied from this point of view by Bugnion [44], behave like ants proceeding in a column. Absolutely blind, these insects display an activity which is partly nocturnal and partly diurnal; they come out at night and return in the morning. They move about in regular ranks, every individual leaving a blackish trail; the troop follows always the same path. If this is swept, the termites are completely disoriented: an indubitable olfactory cue seems to play the sole part.

2.—MOLLUSCS

Various molluscs have formed the subject of sufficiently detailed studies. The limpets, marine Gastropods which live singly, occupy a special site on the rocks; they leave this at times, go and browse on the neighbouring algæ, and then return to their point of departure. This is exactly localized. It is a depression, very little marked on hard rock, but very visible and constituting a veritable nest on rocks of soft substance. The contours of the depression are closely adjusted to those of the shell. The adjustment results from the fact that the mollusc hollows out the rock by scraping with its radula, and that the edge of the shell, as it grows, moulds itself on the contours of this depression. Should the edges of the shell become broken, they regenerate rapidly, always following the contour of the "nest". In consequence, not only does the limpet possess a fixed site, which it returns to re-occupy when it has been away, but it always takes the same relative position on this site.

Limpets move abroad periodically, and their displacements are of an alimentary order. This fact, established by Aristotle, and confirmed by Réaumur, has often been verified since. The displacement is often effected on dry land, at low tide, and according to the statements of Lloyd Morgan [41], Davis [12], and Piéron [44], it can reach a length of 90 centimetres; but it is also carried out under water at high tide (Jeffreys [46], Gemmill [14], Willcox [47], Piéron). Everything depends on the prevailing conditions, and notably on conditions of humidity; the limpets move about at low tide only in sufficiently humid circumstances.

The fact of displacement under the water at high tide is worthy of emphasis. It destroys, in fact, the utilitarian explanation sometimes given to account for the existence of a nest. According to this interpretation the nest would, by means of its contours adjusted to those of the shell, permit the mollusc to adhere very strongly to its substratum, and to resist violent shocks of the waves. If such were the case, the mollusc ought not to leave its nest at high tide, since it is precisely when it is moving about that it would run the risk of being dislodged from its shell and tossed about But it is known that the limpets adhere very firmly to their substratum and all the more firmly when they undergo shocks The musculature of their foot suffices to ensure this, without the necessity for the edge of the shell to coincide with the contours of a rock depression. This circumstance renders problematic the utility of the nest for the limpet, and gives a very general significance to the phenomenon of orientation.

However it may be the " nest " exists ; the limpets leave and return to it ; they return constantly, and each time re-adjust themselves to the contours of the depression. The fact was observed by Lukis as far back as 1831, and has since been seen again by Hawkshaw (1878), Ainsworth Davis, Lloyd Morgan and Piéron The path of return is identical with that of the outward journey ; when the mollusc ceases feeding, it veers round 180° in relation to the direction of the outward journey and starts off again, whilst its tentacles beat constantly as if they were exploring the route.

Olfaction cannot be advanced as a cause; the cutting of the tentacles and the washing of the track effected by Davis neither hindered nor confused the return. On the contrary, the experiments of Piéron bring out the *rôle* of touch An obstacle on the path of return determines first of all a halt, then lengthy waverings to right and to left, and when the limpets finally pass it is at the end of one or several hours By scraping the path over a certain length there is provoked similarly a halt and prolonged waverings; the crossing of the altered space takes place only after a very long time

The modification of the ground suffices then to disorient the molluscs, and such modification can only affect tactile cues. However, no special imprint is noticed; and one must particularly reject the hypothesis that the mollusc traces a path on the outward journey by means of its radula, and follows it on return What the mollusc registers are rather the various features of the surface over which it moves,

These same cues, moreover, seem to come into play when the animal, having regained its nest, fits the contours of its shell into those of its site. If the fitting exacted, for its carrying-out, that the parts adjusting themselves should both be intact, one would have to admit a strictly mechanical process. But it is in no wise the case; the limpets resume their place exactly, and orientate themselves in identical fashion, even if the edges of the shell, more or less broken, no longer coincide with the interior contours of the nest, provided the latter remain intact.

If they are not intact, what happens? It all depends on the part which is modified. If the circumference only is affected, so that fitting of the shell is no longer possible, the limpets none the less take their exact position. The position is similarly taken if the deformation affects half the site, the other half remaining unaltered, or if, the circumference not having been touched, the centre is demolished. Briefly, the position is always resumed when the site is partially intact. When it is entirely altered the limpets halt, approximately at the place their nest formerly occupied; but they do not resume their habitual position.

Tactile cues, recognized perhaps by the pallial tentacles, or by the sole of the foot, can then hardly be doubted. Nevertheless, since the limpets find their nest site, at least approximately, even when this site is entirely confused, cues of another order necessarily enter into play. In effect, observation shows that the limpets register, besides the images closely confined to the path traversed, other images bearing on the immediate or nearly immediate surroundings of the nest. If, for example, several individuals are carried a distance from the nest, varying between 4 and 20 centimetres, and in divers directions, some of them regain the nest site and the number of these seems proportional to the distance. Thus:

Out of 6 limpets placed 4 centimetres away, 5 regained the nest,
„ 5 „ 10 „ „ 3 „ „
„ 9 „ between 10 and 20 „ „ 2 „ „

results very comparable with those which are obtained for the Hymenoptera. Of course, it is possible that the images registered may be tactile images. Further, as a limpet cannot browse indefinitely on the same Algæ, it learns perforce to know from a tactile point of view the surroundings of its nest within a certain radius.

Nevertheless, it apparently also registers visual images. The following experiment furnishes an indication of this. Whilst a limpet is moving about on an entirely smooth schist boulder, the latter is turned through 180°; the animal halts immediately, remains motionless for two minutes, then makes a half-turn, and resumes its initial direction. Recommenced a second time, the experiment gives the same result.

The slope of the ground also exercises an influence, as in the case of the ants. If, whilst a limpet is descending a schist boulder, the inclination is reversed by turning it 180° on its horizontal axis, the mollusc halts, then turns round and resumes the movement of descent. This influence is exercised very strongly.

and dominates that of the light. Thus it happens that a limpet descending a slope inclined 25° to the horizontal, with the sun behind, halts when the inclination is reversed, then wavers a little, and finally turns round and resumes its direction.

Tactile cues of course predominate incontestably in the limpets' return to the nest. And this is in keeping with the mode of organization of the animal, which effects close relations with its substratum by means of its pallial tentacles and the sole of its foot

3.—VARIOUS OTHER MOLLUSCS

Other molluscs, the *Calyptræa* studied by Piéron, the *Siphonaria* (*Siphonaria alternata*) and the *Fissurella* (*Fissurella barbadensis*) studied by Willcox, the *Helcion* (*Helcion pellucidum*) studied by Piéron, have also a fixed nest site from which they rove at intervals, and which they re-find probably by the aid of tactile cues.

Similarly, the *Chiton* studied by Crozier[44] leaves its nest, sometimes going to a distance of one and a half metres. It seems to be guided by the light; in any case its return is, in some measure, connected with the distance. If transported beyond about one and a half metres, it does not return, but adopts a new home.

Thus, all the Invertebrates which have a "nest", and which leave it, utilize sensory cues comparable with one another. According to the species and the conditions, these cues are visual, olfactory, tactile, baræsthetic or kinæsthetic, but all are of a sensory order. They correspond to the registration of images taken from the external world, and existing within the domain of man's apprehension. Nothing leads us to suppose that anyone whatever of these Invertebrates makes use of images corresponding to a sense-organ peculiar to it alone, and to stimuli to which it alone can be sensitive.

It now remains to examine how the Vertebrates behave in this respect.

CHAPTER V

ORIENTATION IN THE VERTEBRATES

PARADOXICAL as it may seem, as far as the Vertebrates are concerned, we possess far fewer sure data than for the Invertebrates. Experimental research encounters various difficulties, and has hardly been pursued in a really systematic fashion. Too often, the assertions made on the return of Vertebrates to the nest, proceed from observations made without rigorous control, interpreted by the help of preconceived opinions, or of superfluous hypotheses which the observer takes for facts. And, definitely, the most precise information we possess on the phenomenon of orientation in the Vertebrates, is that which we deduce from results obtained by research on the Invertebrates.[1]

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[1] It is convenient to state here, in order to show the diversity of process, the way in which certain spiders, notably *Argiope brunnichi*, which I have specially observed (40), regain the web, which they left at the moment of laying. The spiders in general move afield unrolling a thread fixed to their web; this can easily be demonstrated. They proceed in the same way whatever the distance which separates them from their point of departure. Then they take up the thread in the reverse direction. Nothing is simpler. It is merely necessary to remark that this return offers no advantage to the spider, since it respins its web constantly, and the place where it spins this has not the least importance.

The *Argiope* builds its nest at a distance; once constructed, it is abandoned. The spider could, having laid its eggs, set up the web

Certainly it is not a question of drawing conclusions from one to the other; too considerable a distance separates them. Nevertheless, no difference in kind exists between them, and the fundamental resemblances which connect the nervous systems of the various animals permit, at least, comparisons which may be suggestive.

At the outset, a distinction must be made. In many Vertebrates the phenomenon of *migration* is observed, and it is necessary to avoid confusing this with *orientation*. The confusion is quite often made, and various observers have attempted to "explain" the second phenomenon by the first. The explanation consists in saying that migration depends on an "hereditary topographical memory" of which orientation would be a residuum. That migrations involve an hereditary memory, it is claimed to demonstrate by the following observations, taken from Gaetke.[illegible] In 328 species of migratory birds observed, it was found that the young left the region in which they were born six to eight weeks *before* the parents, and directed themselves exactly towards the regions these latter would shortly afterwards regain. The observation is certainly exact, but the interpretation goes beyond the facts, and proceeds from faulty analysis.

no matter where, under similar conditions, however, it returns to the previously abandoned web. Nothing proves, moreover, that this return is constant, without doubt it comes about that the thread attached to the spinnerets is broken at the time of manufacturing the egg-sac

What is migration? It is a periodic displacement, seasonal or otherwise, under the incontestable influence of stimulation from the surroundings—temperature, illumination, hygrometric state, etc.—and may be a function or not of physiological states These stimuli affect the young equally with the parents, perhaps with even greater intensity. In consequence, the young behave as the parents do, and independently of them Furthermore, since they set out from the same region as that from which the parents will later set out, all the chances are in favour of their arriving at the same destination, or in its neighbourhood As for the parents, not only are they subject to the same stimuli, but in addition they have registered local cues, so much so that, brought back to a given region, they return often and very exactly to the same spot It is from the moment that the birds approach a known region that migration and orientation coincide, or rather that orientation is substituted for migration. Up till then the phenomenon consists less in returning to a point of departure than in leaving a region become uninhabitable. Migration and orientation remain entirely distinct.

I.—THE CARRIER PIGEON

The carrier pigeon has formed the subject of the majority of publications treating of orientation in the Vertebrates. To tell the truth, these publications contain for the most part data mainly gathered without method and difficult to utilize. And if the remainder are less subject to the need for caution very few furnish complete results.

All these very disparate data group themselves around two principal facts:

(*a*) The pigeon regains the cote even when transported to a great distance,

(*b*) It regains the cote even if it has never accomplished the outward journey by its own efforts.

To account for these facts authors are separated according to four principal tendencies:

The pigeon is considered to orientate itself by reason of a magnetic or electro-magnetic sensibility;

It takes on the return the reverse of the outward journey;

It possesses a special sense entirely *sui generis*;

It utilizes ordinary sensory cues.

A.—The hypotheses

A first hypothesis, the existence of a *magnetic sense*, formulated primarily by Viguier, has been developed by Thauziès, notably in 1909[41]. It attracts a considerable number of pigeon fanciers.

Thauziès rejects the idea that the pigeon might conserve the memory of places, and be guided by visual cues. He bases his denial on various considerations.

If, he says, the pigeon made use of such cues, it could see them only by rising very high at the moment of release, and all the higher in proportion as the goal to be reached is further away. Sometimes it would need to rise to a height of several kilometres. Now, the pigeon mounts, on a maximum, to a height of 300 metres.

In the second place, when the apprenticeship begins, and when for the first time the pigeon is released 2 or 3 kilometres away from the cote, it rises and turns for some time, for from 5 to 15 minutes, as if it did not see the nearby cote, and very often it departs in the wrong direction. The "hesitation" diminishes at the second release, effected 3 or 4 kilometres further away. It hardly exists further at the fifth release, at a distance of about 40 kilometres. The pigeon can then be sent to a distance of 100 kilometres, then to 250; it can finally be released in various directions: it returns in a straight line. If it has served its apprenticeship to the north of the cote, it returns even if transported to the south, and *vice versa*. Sight, concludes Thauziès, hardly enters into all this, and it is necessary to think of some other factor. The author supposes that the pigeon directs itself by means of electromagnetic currents. This amounts to saying, and such is the author's opinion, that the pigeon is a bird eminently sensitive to influences of this order.

Do any indications exist in support of this hypothesis? To tell the truth, the indications are reduced to vague assumptions. The influence of a zone of storms or fog is said to be exercised at a great distance—80, 100 or 200 kilometres—and to disturb the pigeons even if at the point of liberation the sky is clear. Thus, some well-trained pigeons, released at Orleans in fine weather with a light southerly wind, found their way badly. They should have returned at mid-day; 11 only returned before night, and the rest the next day. It seems that a similar experience was had with all releases made the same day. Now, on that particular day, an abnormal electric situation was noticed, with magnetic storms on the Pic du Midi, that is to say, 1,000 kilometres away. In addition, every atmospheric disturbance inappreciable except by very sensitive apparatus is claimed to disturb the pigeon, which is said to take much more time, even to the extent of double the time, to return.

Fresh assumptions result from observations of another nature; the orientation of the pigeon is said to be more prompt in the morning than in the afternoon; it is said to be difficult when the release coincides with a change of the moon; finally a pigeon left at rest for five or six months, then released at a great distance, either does not return or returns slowly, even in a known region.

All these accumulated conjectures hardly lead to certitude. Even supposing that the enumerated influences act on the pigeon, nothing indicates that they serve as cues, or that the stated disturbances proceed from an action exercised *directly* on orientation. Moreover, Maurain [illegible], taking up as a pure physicist, and without prejudice the hypothesis of magnetism, shows its extreme weakness. First of all he remarks that magnetic storms are fairly localized, and that the pigeons could not be affected by them, unless possessed of an extreme hypersensibility. Now, the constituent substances of living matter are but little sensitive to influences of this order, the magnetic field of strong electro-magnets having no more action on the Vertebrates than on the Protozoa. In addition, in large towns, and at times also in the country, the terrestrial magnetic field is disturbed by the electro-magnetic influences emitted by the electric cables, the pigeons hardly appear disoriented.

Nor is this all. If the pigeon possessed a "magnetic sense" it would orientate itself in function of the magnetic declination, *knowing* the spot at which it finds itself. This is a difficult calculation; and much is based precisely on the ignorance in which the pigeon is said to be of the places where it is released. Could the pigeon be sufficiently sensitive to magnetic variations to appreciate changes in declination and inclination? On what ground can it be supposed? Besides the fact that the differences are slight and the magnetic field weak, the smallest magnetized bar being at least ten times stronger, the pigeon is insensitive to very strong magnetic fields [1]

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[1] As for electric influences, they are so unstable in time and space that they cannot serve as landmarks.

There is hardly need to add anything to these decisive arguments of Maurain. Let us mention, nevertheless, the experiment of Arcy, who furnishes confirmation. Some pigeons transported in a case were subjected, in the course of the journey, to magnetic, electric and calorific influences in such a way that they were unable to take cues from the analogous normal influences. Released in an unknown zone, 10 kilometres from the cote, these pigeons returned in twenty minutes Without doubt they could have traversed about 25 kilometres in the same time, but they had none the less found for the return cues quite other than magnetic ones

The hypothesis of a magnetic sense seems, then, quite improbable. Where, moreover, could the corresponding sensory organ be situated? In the semi-circular canals? Would those of birds differ in this respect from those of other Vertebrates? For not all of these latter orientate themselves under conditions comparable to those which are known for the pigeon. To assume this would be to make a gratuitous hypothesis; as it would also be to attribute this "magnetic sense" to tactile nerve-endings. To persist in the hypothesis of a magnetic sense is to run the risk of stultifying all research.

Shall we find a solution in the theory of retracement upheld by Reynaud[11]? The theory consists in supposing that the bird registers all the directions followed on the outward journey, even in the case of passive transport, and that it takes, on the return, an exactly superposed path in the reverse direction. The bird would then possess a sense of "attitudes" which would originate in the semi-circular canals; the muscular sense would also intervene.

No fact really exists in support of this hypothesis. At the present time, one is actually no longer able to attribute to the semi-circular canals any part in orientation. As Ewald[14] and quite recently Koenig[14] have shown they contribute to *equilibration*, especially in relation with muscular tonus. Furthermore, Watson[11] points out simply that a pigeon transported in a basket and turned in all directions a great number of times, does not perform these movements of rotation again one by one, when it is liberated. This *reductio ad absurdum* is sufficient in itself.

Is it a question, then, of a "special sense", of a sort of mysterious property which would attach the pigeon to its cote? This is what numerous amateurs maintain. Fabre furnishes them an argument which seeks to be decisive: the *Cerceris* orientates itself at a distance of 3 kilometres; the pigeon is 1,000 times bigger—it ought then to orientate itself at 3,000 kilometres . . . Apart from the fact that the *Cerceris*, without a doubt, makes use of visual cues, the reasoning carries with it its own refutation.[1]

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[1] Quite recently M. Jean Cassamajor[12] has developed the idea that the carrier pigeon may register as cues waves of a given length emitted in the region of the cote. Sensitive to these waves, the pigeon would undergo their influence at a great distance.

B.—Sensory cues

None of the theories advanced gives, then, the solution of the problem. The analysis of the facts must perforce be resumed, in the attempt to draw from them a conclusion, at least a provisional one.

First of all, what is the carrier pigeon?

By reading diverse information furnished by the pigeon fanciers, one succeeds in forming for oneself a very precise idea on this point. If all pigeons are capable of returning to their cote when they fly some kilometres from it, not all are equally capable of orientating themselves at very great distances. In this respect it can be said that orientation is an individual accomplishment. Perhaps it depends on some quality of unknown nature; in all cases the selection effected by the trainers is based on two definitely appreciable criteria: great muscular vigour and good sight. The muscular vigour permits journeys to great distances; and does not good sight have for the bird a relation with the fact of scanning the landscape and registering visual landmarks?

It is very necessary also to point out that "good sight" implies for a bird a possibility of vision hardly

According to M. Casamajor, this special sensibility would be expressed by the intermediary of the nerve-endings of the inner ear. This hypothesis differs appreciably from the old electro-magnetic theory, although it calls forth various objections, it cannot be rejected *a priori*, and we must await the results of experiments in progress imagined by man. In relation with ours, the visual acuity of birds is in general incomparable; that of the pigeon ranks among the best. Without doubt there are marked individual differences; but we must rest assured that selection is effected among animals whose sight is excellent.

Given these two qualities the pigeon undergoes rearing and training; it is habituated to travel distances and to find its nourishment in the course of the journey.

The rearing is carried out, as we know, in successive stages. Is it purely muscular training? The idea cannot be eliminated that the pigeon at the same time acquires knowledge of places, without doubt over a sufficiently large area. Its sight ranges around and the images it registers are those of a landscape extending widely to right and to left, before and behind.

The training finished, the pigeon regains its cote from whatever spot it may have been transported to, and even if it has never actively made the journey. The fact is certain. The conditions of such returns must now be made clear. They are effected better and more regularly the shorter the distance. According to Dusolier[47], who sums up a mass of data, pigeons taken to a distance of 1,200 kilometres return with great delay, a number of them not returning at all; the same happens each time the pigeon is taken beyond 800 to 1,000 kilometres; the optimum distance would appear not to pass 300 kilometres.

Various conditions hinder the return. Notably the pigeons lose themselves in time of snow, and one can, with Guibert, attribute this result to the change undergone by the landscape. Mist produces the same result. According to de Roo and other pigeon fanciers this result would depend on an electric disturbance. Electric conductivity does, of course, diminish in fog; but the interpretation nevertheless does not seem exact, since the mist has effect only in so far as it obscures the landscape. Thus, pigeons released at sea, in a fog, rise above it; if the mist is limited to the sea and they can perceive the land, they orientate themselves. In these conditions, the part played by visual cues seems scarcely to be disputable. Schneider[illegible] furthermore recognizes that these cues are groups of houses, hills, small woods, etc., that is to say, not details, but groups of objects visible from a great distance.

However, a grave objection remains, released in an unknown zone, the pigeons find their way to the cote. There are even cited truly remarkable facts of this order. Dusolier[illegible], for example, reports the following: two pigeons raised at Paris and kept without training till the age of three and a half years, were taken to Périgord. There they were shut up for a month Liberated at this time, they both regained Paris in less than two days. This is a precise fact; but it does not, by itself, authorize any conclusion. A very strict analysis of this and of analogous facts, remains necessary. We possess some data enabling us to proceed with this.

The question poses itself in the following way. Will all the pigeons released in an unknown region return, and in what time will they do so? An experiment on a large scale made in 1895 furnishes information on this subject. 5,000 pigeons were released at sea, at distances 146, 200, 300 and 500 kilometres west of Croisic The speed of the return diminished with the distance, it was from 75 to 88 kilometres an hour for 200 kilometres, 60 for 300, and barely 40 for 500. The altitude of the flight increased with the distance from land; it was sufficiently great, when the liberation was effected at 500 kilometres, for the pigeons to be invisible to the naked eye As for the number of returns, this diminished with the distance. Out of 1,500 pigeons released at 500 kilometres, 300 returned at the end of forty-eight hours; the others were found scattered everywhere, in England, Spain, Portugal, Algeria, at Cape Verde, in Egypt, and in the Caucasus In short, return to the point of departure became a matter of chance.

Another experiment, although of much smaller extent, is no less significant; 8 pigeons, ignorant of the way, were transported from Antwerp to London. Released at 6 o'clock in the morning, in fine weather, they turned about for a long time, and then flew off and had returned to Antwerp by seven in the evening, having taken thirteen hours to accomplish a journey normally requiring barely three.

The following experiment, due to Thauziès[11], is also strongly suggestive. There were transported to Geneva 24 pigeons, stationed at Versailles, 38 pigeons stationed at Guéret, and 8 pigeons stationed at Gannat. All had undergone training in a very different direction from that of the journey they had to accomplish. Here are the results:

The 24 pigeons from Versailles were liberated at 7.10 a.m. on the 6th of August; 2 returned the same day at 5.46 p.m.; 9 returned on the 7th of August between 6.20 a.m. and 6.15 p.m.; all the rest returned on the 10th of August.

Of the 38 pigeons from Guéret "about two-thirds" returned the same day between 12.15 and 12.50 p.m., and the rest the next day.

Finally, of the 8 pigeons from Gannat, none returned on the day of liberating. 3 returned on the 7th at 6.9 a.m., 7.12 a.m., and 12.50 p.m.; the others returned on the 8th at 7.57 a.m., on the 9th at 3 p.m., on the 11th at 4 p.m., and on the 12th at 10 a.m.; the eighth did not return. Such results are sufficiently eloquent. Admittedly the counter-experiment, which would consist in taking all the pigeons back to Geneva and releasing them a second time, is lacking. Nevertheless, this slowness of return hardly implies a very sure sense of orientation, and one conceives rather of birds wandering at hazard and finally encountering some landmark which puts them on the way.[1]

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[1] Thauziès emphasizes the difficulties of the journey by reason of the accidents of the land, but these difficulties seem very illusory.

To these experiments should be added that of Watson and Lashley with the terns[11] Transported 855 miles from their nest, these birds had returned at the end of from six to eleven days, in the proportion of three out of ten. At a lesser distance visual memory seemed to play a preponderant *rôle*.

To sum up, the fact seems general. "Good" pigeons, well-trained, and released in an unknown region, when they return never do so within a normal time, and those which do return are those which have flown about the most, having thus multiplied the chances of encountering cues.

These chances, of course, diminish with the distance. If, for instance, there are liberated, 400 kilometres out at sea, pigeons trained on the line Bordeaux-Nantes, the straight lines from the point of release to the two termini delimit an angle of about 45°, which represents an eighth of the circumference (of a circle) traced around the point of departure taken as a centre. Every pigeon has therefore one chance in eight of being in a known area. The more distant the point of release, the smaller becomes the angle and the more the chances diminish; they are augmented in the contrary case.

There remains, however, one last objection, that of nocturnal flights. Once the sun has sunk, the pigeon does not fly spontaneously; nevertheless, by means of special training one can succeed in making it travel by night. But the observers are in no accord as to the conditions favourable to these journeys.[43] Some are of the opinion that a clear night is better than a dark one; others postulate exactly the contrary. The latter explain, with Thauziès[44], that the moonlight modifies the landscape, and thus confuses the pigeon. Is this not, at the same time, to bring in visual cues? These cues, moreover, are not lacking: even on a dark night, roads, rivers, stretches of water and various features of the land are perfectly perceptible.

Nocturnal journeys, it may be added, hardly achieve a brilliant success. The flight is hesitating, and always quite slow, its speed varying between 460 and 600 metres per minute. Sometimes the result is quite poor, such as the following, reported by Thauziès: 125 pigeons were released on a dark night at 6 p.m., one of them returned at 8.15 p.m., three others during the night, and the majority the next morning at 9 o'clock.

Fundamentally, the objection from nocturnal flights does not exclude the hypothesis of visual cues, an hypothesis supported by the mass of accumulated data; the utilization of these cues seems undeniable. They are doubtless not the only ones, and one must think notably of kinæsthesis. A pigeon trained for a certain distance registers very probably the effort accomplished; it suffices that an incident diminish this effort for the bird to pass beyond the goal. This is what is produced when the pigeon flies with the wind; it goes beyond the cote and must then retrace its course.[illegible] [1]

2.—VARIOUS VERTEBRATES

Besides the pigeons a number of other Vertebrates —birds or mammals—regain the shelter which they have left Apparently they make use of sensory cues, notably visual ones.

Numerous "facts" would nevertheless tend to cause the admission, as for the pigeons, of the existence of a special sense, an absolute sense of direction. But it is necessary to be on guard against accepting these "facts" without serious control. Here are two cases in point. Yung [illegible] learned that a young cat transported to a considerable distance (50 kilometres), was said to have regained rapidly its point of departure The case was too remarkable not to be checked After inquiry, it had to be recognised that the cat had not left its new domicile; a confusion had simply arisen between two more or less similar cats

The second example, shows equally, but in another way, how easily observers overlook an important circumstance Vineq [illegible] relates that after having made 12 kilometres on foot to reach a railway station, then 15 kilometres in the train, and after having gone about the town, a dog finally became lost in the streets. He nevertheless returned late at night. Now, adds the author, this dog knew only the country around the house, within a radius of 6 kilometres. But he forgets at the least the 12 kilometres made on foot; he forgets the windings and turnings made in the town, leading back perforce to the station, the landmark and point of departure.

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[1] It is useless to detain ourselves with the question of the recognition of the cote itself; it is not connected with the flight in general direction, and the arrival in the region of the site, by these tokens that, in the case of flights at night, the cote must be illuminated, or else the pigeon does not return. The visual cue is evident here.

Thus frequently the fact reported is incompletely observed; account is taken solely of the incidents capable of leading the animal astray, these are insisted on, without any attempt to evaluate the incidents capable of aiding it to return towards its home.

This is certainly also the case for a large number of analogous facts. Many are "historical", which amounts to saying "legendary"; one divines only too well their insufficiency. On the other hand, well-observed facts bring out for the mammals the utilization of visual cues. Claparède[47] cites the case of a young cat, ten months old, losing itself 350 metres from its home, yet it seems that the sense of direction should play a special part at so short a distance. Houzeau[48] reports a personal experience. Exploring an unknown region on horseback, he covered ten kilometres, making numerous turns and detours. Finally he lost his way. The sky was overcast, and he had no compass. Unable to find his way, he abandoned himself to his horse. The latter picked up the outward track, and returned to the point of departure. The evidence imposes itself that the horse must have registered visual cues; and the possibility of registering them with such abundance and precision implies a remarkable memory.

This example confirms various accounts of the same order. It permits the doubting, not of the good faith, but of the powers of observation of writers who speak of horses returning to the stable by following roads entirely distinct from the outward track. The actual fact is very possible, but shorn of a certain number of accessory circumstances, it loses all value.

It is the same for the dog. Houzeau analyses closely the behaviour of young dogs (four to six months old) intentionally turned astray in the course of their *first outing*. First of all the sense of smell comes into play; the dogs sniff the trail, and if this olfactory cue does not suffice, they retrace by sight the outward path, passing clearly from one cue to another. However, in flat country, when the simultaneous sight of several landmarks is possible, they often follow the shortest path. Among other examples, the author cites that of a dog of five months, which had been led to a distance, after having been made to cross a river over a tree-trunk. Fearing the water, the animal on return ran hither and thither until, after a long time, it finished by re-finding the improvised bridge.

Quite recently, Richardson[44] has completely confirmed these conclusions in regard to orientation in the dog.

Man also behaves no differently. Accompanied by a young Indian of ten years, Bates[10] was lost in a forest. The child retraced the path by which they came, having unconsciously noted a series of landmarks which Bates himself had not remarked. In his turn von den Steinen[11] cites the case of a native of Brazil who remembered all the peculiarities of the course of a river. He recognized each bend, indicating its relative situation, and noted the position of certain trees. He registered thus a series of cues, without apparent importance considered separately, but forming a whole This same man was incapable of counting beyond two or three, or of constructing a logical argument.

CHAPTER VI

GENERAL SUMMARY

IF we now cast a general glance over the actually known facts, and if we try to discover the bond which unites them, we shall be immediately struck by the analogy which allies all animals. The facts based upon well-conducted experiments or observations constantly reduce the phenomena of orientation and of place-recognition to processes of sensory memory, bringing into play the organs of the ordinary senses

If there are observations the interpretation of which appears delicate, such as the homing of pigeons liberated in an unknown region, none of them presents itself in a sufficiently rigorous manner to set aside the idea of pure sensory memory. And even comparing the different animals with one another, the similarity is such that we feel led to accept for the ones the conclusions that the facts impose for the others Wasps liberated in an unknown zone turn about for a long time above the point of release ; *nothing attracts them* in one direction or another ; they wander at hazard, undergoing various contingencies, and some are definitely lost, while others encounter some cue thanks to which they again find the nest. Pigeons behave in the same way; almost as soon as liberated they turn this way and that, then set off in one direction or another, the number of those losing the way being increased with the distance, that is to say, at the same time as the chances of meeting a landmark are diminished. Of course there are fortunate cases, which are moreover exceptional; but they detract nothing from the value of this resemblance between diverse organisms. However separated they may be, from various points of view, their nervous systems possess general common properties, of which the importance cannot be overlooked.

As for the cues, the study of the Invertebrates, and especially of the insects, shows that some or others predominate, or pass to the second rank, according to the animals and according to the circumstances for the same animals. Ants make use of olfactory cues when moving abroad in a column, but when the trail gives out, luminous cues hitherto accessory acquire primary importance. The limpet makes use especially of tactile cues, whilst flying Hymenoptera use hardly anything but visual cues until the moment of arrival at the nest itself. In fact, all the sense-organs take part simultaneously or successively in the phenomenon. All register varied images, and these images are associated with one another, forming a complex in the nervous system of the animal.

None of these images appears to remain isolated. Every one of them is a guide only in so far as it is associated with the others, or forms an integral part of the complex. It is thus that the nest itself, it would seem, exists for the animal only as a function of the complete whole. And it matters little, from this point of view, whether or no the images which represent it are of the same nature as those which give the general direction, and allow the recognition of a certain site. The narration of the facts does, indeed, lead us to speak as if the cote were for the pigeon an independent and isolated landmark; different observers are astonished that the bird although able to perceive it at the point of liberation, behaves as an animal which has lost the way, and does not head directly for the cote. This signifies precisely that the cote belongs to the complex and has reality for the pigeon, as in the case of the nest for the Hymenopteron, only as connected with the whole. All takes place as if the image of the cote corresponded to a topographical relation, of which all the cues giving the general direction and the site form a part. The pigeon which goes out for the first time has not been able to register these relations of the cote with the environment, the elaboration of the complex is effected with variable rapidity in the course of successive outings. And the processes seem very analogous in the case of the Hymenoptera; the nest or the hive, when moved backwards, is not immediately recognized. The insects go straight to the site, which represents for them part of a whole, a part which is just as much a relation of distance as an actual object.

Is this complex, whatever it may be, established in a rigid and perfectly irreducible manner? Does *A* evoke *B*, and *B* evoke *C*, in such a way that the animal must re-pass all the points of a track it has once traversed? The facts prove that this is not the case. The connection between the cues has, on the other hand, quite a flexibility; it bears only on the order of sequence, without necessarily implying an immediate succession. For the animal to go towards *C*, it suffices for *C* to follow *A*, even if *B* has disappeared Better still, circumstances, or simply habit, can lead the animal to suppress immediate connections and to simplify the complexes Everything occurs as though the image of *A* evoked several successive images, and as though the interposed images merged progressively, and finally disappeared in such a way that *C* or *D*, or any other, came immediately in the train of *A* In open country, for example, the dog takes the straight line between two widely separated cues; bees, wasps and ants proceed in the same way . . . In short, the elaboration of the complex of images is such that the nest site becomes connected, not in an isolated manner with one or another of the parts of the complex, but with every one of them, that is to say, with the complex in its entirety.

Thus is constituted the "bee line" or the "crow flight", which becomes ultimately more or less kinæsthetic. For visual, olfactory, or other images there is substituted the memory of a certain muscular effort, which the animal accomplishes in known territory, without the constant aid of exterior cues

In sum, memory plays a very important and probably a preponderant *rôle* in the process of orientation Whether one envisages a mollusc, an insect, a mammal, or man himself, one really perceives no essential difference among them in this respect Whether it wishes or not, the animal is directly influenced by the outside world, it registers the images of surrounding objects, and these images assume for it various relations The registration and elaboration are effected with surprising rapidity A single journey suffices for an Indian, as for a horse or any other animal, to retain the memory of the path traversed In this respect, a truly striking difference is remarked between educated man, inclined to the various preoccupations occasioned by contemporary civilization, and uncivilized man, whose every effort is bent on reaping benefit from nature by the least complicated means The latter lives more outside himself; nothing escapes him of external phenomena, and, relatively little distracted, he consciously or not observes everything, registering it and elaborating multiple images

To be sure, in this process of registration and elaboration, all the senses intervene in various degrees, but nothing authorizes the assumption that to the ordinary senses are added others in more immediate relation with this process. If we proceed to anatomical and physiological analysis of a pigeon, for example, we are easily convinced that sight dominates its behaviour when it orientates itself. In its case vision is very specially acute; it embraces a very extended field, and carries far On the other hand, its auditory acuity differs little from that of man; the sense of smell is exercised feebly and to a short distance; in addition, the tactile nerve-endings, whatever their exact function may be, are hardly subject to the influence of stimuli placed at a very great distance As for the semi-circular canals, they contribute to the maintenance of muscular tonus, and though their stimulation is able to affect equilibration, and thus modify motor activity, they exercise no direct action on the possibility of return towards the cote. As for a "special" sense, we see hardly any sign of this; at least we are unable to perceive its anatomical basis, and this fact suffices in itself

It is thus for all the animals. Whether one proceeds by direct experimental analysis, or by elimination, one is constantly led to cues registered by the ordinary sense-organs, with this simple reserve, that the homologous organs do not predominate equally in all cases

Having arrived at this conclusion, shall we be able to go further and consider the question entirely solved?

The problem is certainly not exhausted Many points remain obscure, which demand a fresh effort at analysis by means of a particularly rigorous method of research. The essential thing is to put aside all preconceived ideas, and to affirm nothing which does not rest on a positive proof. Doubtless many facts of singular aspect appear inexplicable by customary methods, and in the present state of our knowledge. The pigeon which crosses hundreds of kilometres of unknown country, and returns to the cote, gives us lively surprise; and we willingly see a certain mystery cast about it. In our astonishment we forget all the cases in which in analogous circumstances a pigeon has not reappeared We retain certain facts to the exclusion of others, without asking ourselves whether the exceptional cases radically oppose all the rest, or whether they are only particular instances of a general phenomenon.

In renouncing all hasty interpretation and every unfounded hypothesis we leave the field free for research, and preserve the possibility of arriving at a solution.

REFERENCES

[1] Henri Piéron. Psychologie zoologique. In *Traité de Psychologie*, G. Dumas, t. II, 1925.

[2] T. H. Huxley. *L'Écrevisse, Introduction à l'étude de la Zoologie*. Paris, 1896

[3] Gaston Bonnier. Le sens de la direction chez les abeilles. *C. R. Acad. Sci.*, 1909.

[4] C. H. Turner, Homing of Burrowing Bees. *Biol. Bull.*, 1908

[5] A. Bethe. Durfen wir den Ameisen und Bienen psychische Qualitaten zuschreiben? *Arch. f. ges. Phys.*, 1898.

[6] A. Descy. Observations sur le retour au nid des Hyménoptères, 1re partie. *Bull. Soc. ent. Belge*, 1922.

[7] L. Verlaine. L'instinct et l'intelligence chez les Hyménoptères. I. Le problème du retour au nid et de la reconnaissance du nid. *Mém. publ. par Acad. roy. Belg.*, t. VIII, 1924.

[8] Étienne Rabaud. Reconnaissance du nid et des lieux chez les Insectes. *Journal de Psychologie*, 1920.

[9] J. H. Fabre. *Souvenirs entomologiques*, Paris.

[10] John Lubbock. *Fourmis, Abeilles et Guêpes*, t. II, Paris, 1883

[11] H. von Buttel-Reepen. Sind die Bienen Reflexmaschinen? *Biol. Zentr.*, 1900

[12] Romanes, in *Les sens et l'instinct chez les animaux*, J. Lubbock. Paris, 1891.

[13] E. Yung. Un sens mystérieux: le sens du retour. *Semaine littéraire de Genève*, 1898.

[14] Étienne Rabaud. Le retour au nid de *Vespa sylvestris* *Feuille des Naturalistes*, 1924.

C. Ferton. Notes détachées sur l'instinct des Hyménoptères mellifères et ravisseurs, 3^e série. *Ann. Soc. ent. Fr.*, 1905.

Henri Piéron. A propos des expériences de Ferton. *Bull. Inst. gén. psych.*, 1906.

C. Ferton. Notes détachées, etc., 4^e série. *Ann. Soc. ent. Fr.*, 1908.

Étienne Rabaud. Observations et expériences sur *Ammophila heydeni*. *Bull. Soc. Zool. Fr.*, 1919.

Armand Descy. Instinct et intelligence. Expériences sur l'Ammophila. *Ann. Soc. ent. Belg.*, 1919.

E. L. Bouvier. Les habitudes des Bembex. *Année psychologique*, 1901.

R. Marchand. Sur le retour au nid du *Bembex rostrata*. *Bull. Soc. des Sci. nat. de l'ouest de la France*, 1900.

Étienne Rabaud. Acquisition des habitudes et repères sensoriels chez les Guêpes. *Bull. biol. Fr. et Belgique*, 1926.

Armand Descy. Observations sur le retour au nid des Hyménoptères, 2^e partie. *Bull. Soc. ent. Belg.*, 1922.

C. Ferton. Notes détachées, 3^e série. *Ann. Soc. ent. Fr.*, 1905.

A. Giard. Observations sur l'instinct chez les Hyménoptères. *Bull. Inst. gén. psych.*, 1906.

L. Verlaine. L'instinct et l'intelligence chez les Hyménoptères. III. La reconnaissance du nid et l'éducabilité de l'odorat chez la *Vespa germanica*. *Ann. Soc. roy. Zool. Belg.*, 1925.

R. Brun. Das Orientierungsproblem. *Biol. Zentr.*, 1915, 1916, 1917, 1918, etc. Le problème de l'orientation lointaine chez les Fourmis. *Rev. Suisse de Zool.*, 1916.

A. Forel. Expériences et remarques critiques sur les sensations des Insectes. *Rivista di Scienze biologiche*, 1900-1901.

F. Santschi. Observations et remarques critiques sur le mécanisme de l'orientation chez les Fourmis. *Rev. Suisse de Zool.*, 1911.

Henri Piéron. Le problème de l'orientation envisagé chez les Fourmis. *Scientia*, 1912.

V. Cornetz. *Les explorations et les voyages des Fourmis.* Paris, 1914.

[illegible] F. Santschi. Comment s'orientent les Fourmis. *Rev. Suisse de Zool.*, 1913.

[illegible] C. H. Turner. The Homing of Ants. *Journ. Comp. Neur. and Psych.*, 1907.

[illegible] V. Cornetz. Le sentiment topographique chez les Fourmis. *Revue des Idées*, 1909.

[illegible] V. Cornetz. (*a*) Fourmis dans l'obscurité. *Archives de Psychologie*, 1914
(*b*) Un anniversaire l'expérience de Piéron. *Bulletin Soc. Hist. nat. de l'Af. du N.*, 1925

[illegible] F. Santschi. Remarques nouvelles sur l'orientation des Fourmis *Bull. Soc. Hist. nat. de l'Af. du N.*, 1914

[illegible] Henri Piéron Du rôle du sens musculaire dans l'orientation des Fourmis *Bull. Inst. gén. psych.*, 1904

[illegible] V. Cornetz. Trajets de Fourmis et retour au nid. *Mém. Inst. gén. psych.*, 1910

[illegible] H. Viehmeyer. Beobachtungen uber des Zuruckfinden von Ameisen (*Leptothorax unifasciatus*) zu ihrem Neste. *Illust. Zeitsch. fur Entom.*, 1900.

[illegible] E. Bugnion. Le Termite noir de Ceylan, *Eutermes monoceros*. *Ann. Soc. ent. Fr.*, 1909.

[illegible] C. Lloyd Morgan. The homing of Limpets. *Nature*, 1894.

[illegible] Ainsworth Davis. The habits of the Limpets *Nature*, 1885 and 1895.

[illegible] Henri Piéron Contribution à la biologie de la Patelle et de la Calyptrée. I L'éthologie, les phénomènes sensoriels *Bull. scient. Fr. et Belg.*, 1909. II. Le sens du retour et la mémoire topographique. *Arch. Zool. exp. et gén.*, 1909

[illegible] J. G. Jeffreys. *British Conchology*. London, 1865

[illegible] J. F. Gemmil. On some cases of hermaphroditism in the limpet (*Patella*) with observations regarding the influence of nutrition on sex in the limpet. *Anat. Anzeiger*, 1896.

[illegible] M. A. Willcox. Homing of *Fissurella* and *Siphonaria*. *Science*, 1905.

47 Henri Piéron. Le retour au Home de l'Halcion *Feuille des Naturalistes*, 1925.

[illegible] W. J. Crozier. "Homing" behavior in Chiton. *American Naturalist*, 1921.

[illegible] Étienne Rabaud. Le retour à la toile d'*Argiope bruennichi*. *Feuille des Naturalistes*, 1924.

[illegible] Gaetke. *Die Vogelwarte Helgoland*. Braunschweig, 1900.

[illegible] Thauziès (*a*) L'orientation. *Revue scient.* 1898 ; (*b*) L'orientation lointaine. *Congrès de Psych.*, 1909

[illegible] C. Maurain Enquête sur l'orientation du Pigeon voyageur *La Nature*, 1923.

[illegible] Jean Casamajor. L'orientation du Pigeon voyageur. *La France Colombophile*, 1925 et 1926 (*passim*).

[illegible] Reynaud (*a*) Note sur l'orientation des Oiseaux et le colombier mobile. *Bull. Inst. gén. psych.*, 1903 (*b*) L'orientation des Pigeons voyageurs *Bull Inst. gén. psych.*, 1903.

[illegible] R. Ewald In *Traité élémentaire de physiologie*. Gley, 6e édition, 1925

[illegible] C. J. Koenig Le phosphène normal dans l'étude de l'orientation. *C R. Soc Biol.*, 1923, t. I.

[illegible] Watson. The behavior of noddy and sooty terns. *Science*, 1910.

[illegible] M. Dubolier. Ce que peut faire le pigeon voyageur. *Rev Scient.*, 1903, t II.

[illegible] Schneider Die Orientirung der Brieftaube. *Zeitsch f Psych.*, 1906.

[illegible] M. Dubolier. *Rev Scient.*, 1900.

[illegible] Thauziès Experience d'orientation lointaine *Arch de Psych.*, 1909.

[illegible] J. B. Watson and K. S Lashley An historical and experimental study of homing *Papers of the Carnegie Inst., Dept. of Marine Biology*, 1915

[illegible] Rochon-Duvigneaud and E. Rabaud Enquête sur l'orientation du Pigeon voyageur. *La Nature*, 1926

[illegible] Thauziès. L'orientation lointaine *Revue Scient.*, 1913, t. I.

[illegible] E. Yung A propos de l'orientation chez les chats. *Rev. Scient.*, 1898., t. I.

[illegible] Vineq. Le sens d'orientation chez les animaux. *Rev. Scient.*, 1898, t. I.

[illegible] E. Claparède. Défaut du sens du retour chez un Chat. *Arch. de Psych.*, 1908.

[illegible] J. C. Houzeau. *Études sur les facultés mentales des animaux comparées à celles de l'Homme.* Bruxelles et Leipzig, 1872.

[illegible] E. H. Richardson. The homing instinct in dogs. *Psyche.* 1921

[illegible] H. W. Bates. *The naturalist on the River Amazons.* London, 1873.

[illegible] K. von den Steinen. Unter den Naturvolkern Zentralbrasilien.

N.B.—This list of references contains, of course, only the works it has been thought necessary to use in order to set forth this summary. A complete bibliography of the subject would comprise a veritable volume.

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